
# Modelling the effects of environmental stressors on pig performance

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"*The man who has made the mile record is W.G. George.... His time was 4 minutes 12.75 seconds and the probability is that this record will never be beaten.*" (Harry Andrews 1903 in: Training for Athletics and General Health).

# Dedication

To all who in their own way have contributed

\Ded`i*ca"tion\, n. [L. dedicatio.] **1.** The act of dedicating or the state of being dedicated. **2.** A note prefixed to a literary, artistic, or musical composition dedicating it to someone in token of affection or esteem. **3.** A rite or ceremony of dedicating. **4.** It's what you need if you want to be a record breaker. **5.** Selfless devotion: *served the public with dedication and integrity.*

# Declaration

I hereby declare that this thesis is of my own composition and that all assistance has been duly acknowledged. The results presented herein have not previously been admitted for any other degree or qualification

Ian Jeffrey Wellock

# Acknowledgements

The similarities between the pursuit of a long-distance runner and that of a student completing their PhD thesis at times seem uncannily similar. I should know. It seems fitting therefore to acknowledge those who have helped me complete this thesis with help from quotes obtained from the running books that sit on the shelves in my room as opposed to the usual scientific literature that has adorned my desk this past three years.

For Ilias who's task it has been to guide me in the pursuit of scientific knowledge and who's excellent supervision has helped me to get this far: *"It is one of the strange ironies of this strange life that those who work the hardest, who subject themselves to the strictest discipline, who give up certain pleasurable things in order to achieve a goal, are the happiest men. When you see 20 or 30 men line up for a distance race in some meet, don't pity them, don't feel sorry for them. Better envy them instead."* (Brutus Hamilton, Quoted by Doherty, 1964 in: *Modern Training for Running*). Thanks for the continued inspiration and encouragement. It's been a pleasure.

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For Corinna who has managed to put up with me whilst finishing off this thesis: *"So there I was at the end of 1979: atrophy in the left leg, 'hot spots' up and down the body, a possible stress fracture in the back, and more. And not willing to let some very fine physicians help me. Of course that didn't stop me from running the Honolulu Marathon. The same personality- independent, introverted, single-minded, self-reliant, self-confident, distrusting- that enabled me to excel as an athlete in full health hindered me when I became an athlete in pain."* (Frank Shorter 1984, in: *Olympic Gold. A Runner's Life and Times*). Thanks among many other things for the unbounded patience shown towards a sometimes pain athlete.

Finally for my family back in god's own county: *"Running is the classical road to self-consciousness, self-awareness and self-reliance. Independence is the outstanding characteristic of the runner. He learns the harsh reality of the physical and mental limitations when he runs. He learns that personal commitment, sacrifice and determination are his only means to betterment. Runners only get promoted through self-conquest."* (Noel Carroll, 1981 in: *The Runners Book*). Thanks for letting me get on with it.

# Abstract

The performance of pigs reared commercially is often considerably below that of their potential as seen under good experimental conditions. At least some of this decrease in performance can be attributed to environmental stressors. The aims and corresponding chapters of this thesis were to; (1) Choose a suitable predictor of potential pig growth. (2) Develop a deterministic dynamic model to predict the effects of genotype and the nutritional and thermal environments on the voluntary feed intake, growth and body composition of growing pigs. (3) Test and evaluate the model developed in chapter 2 against experimental data from the literature. (4) Quantify the effects of social stressors on the performance of growing pigs and incorporate these into the previously developed model, including variation in ability to cope with encountered social stressors. (5) Extend the model to deal with individual pig variation. (6) Compare the variation predicted by the population model with that observed under experimental conditions.

The Gompertz function was chosen as a predictor of potential pig growth and as the starting point for model simulation, i.e., to provide an upper limit to growth. It uses few parameters, holds over a wide degree of maturity and the values of its parameters can be estimated simply. Unconstrained voluntary feed intake, predicted from the current state of the pig and composition of the feed, is that required to achieve potential growth. Actual food intake and the consequent gain were predicted taking into account the capacity of the animal to consume bulk and its ability to maintain thermoneutrality. The physical environment, described by the ambient temperature, wind speed, floor type and humidity, sets the maximum and minimum heat the pig is able to lose and determines whether the environment is hot, cold or thermoneutral. Model predictions were generally in good quantitative agreement with the observed data over the wide range of treatments tested and give support to the models value and accuracy. The social environment was described by group size, space allowance, feeder space allowance and the occurrence or not of mixing. All of these factors may act as stressors and it is assumed in the model that they decrease performance by lowering the capacity of the animal to attain its potential. The parameter EX accounts

for differences in ability to cope when exposed to social stressors. The introduction of individual variation in growth potential, initial state and EX allowed the mean population response to be compared with that of the average individual. Whether these responses differed depended in part upon the social stressors encountered. The addition of variation in initial state and EX allowed better estimates of the phenotypic variation observed in real experiments to be achieved.

The developed simulation framework is able to explore, and at least in principle, predict the performance of both individuals and populations differing in growth potential, initial state and ability to cope when raised under given dietary, physical and social environmental conditions. One of the main advantages of simulation models is that they allow the effects of a multiple factors on animal performance to be considered simultaneously, including any interactions that may exist, in a way that cannot be done by direct experimentation. These interactions may be crucial in decision-making processes as different individuals and populations may react differently in response to the same environmental stressors.

# Contents

# List of abbreviations:

*List of the symbols and meanings used in the text*

**Symbols and meanings**

| | | | |
|---|---|---|---|
| A | Whole-body ash content (kg) | $C_{WHC}$ | Animals capacity for water holding capacity (kg/d) |
| ADFI | Average daily feed intake (kg/d) | c | Convective heat transfer coefficient ($W/m^2/°C$) |
| ADG | Average daily gain (kg/d) | DCPC | Digestible crude protein content of diet (g/kg) |
| $ADG_p$ | Maximum rate of average daily gain (kg/d) | DEC | Digestible energy content of diet (MJ/kg) |
| $ADG_s$ | Maximum rate of average daily gain of stressed animal (kg/d) | DM | Dry matter content of diet (kg/kg) |
| $A_a$ | Area of pig in contact with air ($m^2$) | d | Exponent for calculating lipid content of gain |
| $A_c$ | Area of pig in contact with other pig ($m^2$) | dA/dt | Whole-body ash deposition (kg/d) |
| $A_f$ | Area of skin in contact with floor ($m^2$) | $(dA/dt)_{max}$ | Maximum rate of whole-body ash deposition (kg/d) |
| $A_w$ | Area of wet skin ($m^2$) | dBW/dt | Whole body gain (kg/d) |
| a | Exponent for calculating ash content of gain | dEBW/dt | Empty body gain (kg/d) |
| B | Gompertz coefficient of growth ($d^{-1}$) | dL/dt | Whole-body lipid deposition (kg/d) |
| BF | Backfat depth (mm) | $(dL/dt)_{des}$ | Desired rate of whole body lipid deposition (kg/d) |
| BW | Bodyweight (kg) | dP/dt | Whole-body protein deposition (kg/d) |
| $BW_f$ | Final body weight (kg) | $(dP/dt)_{max}$ | Maximum rate of whole-body protein deposition (kg/d) |
| $BW_0$ | Initial body weight (kg) | dW/dt | Daily whole-body water deposition (kg/d) |
| B* | Scaled rate parameter | $(dW/dt)_{max}$ | Maximum rate of whole-body water deposition (kg/d) |
| $b_l$ | Energy required per unit lipid deposition (MJ/kg) | EBW | Empty body weight (kg) |
| $b_p$ | Energy required per unit protein deposition (MJ/kg) | EEC | Effective energy content of diet (MJ/kg) |
| $b_1$ | Constant relating relative daily gain due to space allowance with potential relative daily gain | EI | Energy intake (MJ EE/d) |
| $b_2$ | Constant relating relative daily gain due to group size with potential relative daily gain | EX | Ability to cope when exposed to social stressors |
| $b_3$ | Constant relating relative daily gain due to mixing with potential relative daily gain | $E_{maint}$ | Maintenance energy requirement (MJ/d) |
| $b_4$ | Parameter determining degree of correlation between initial body weight and scaled rate parameter | $E_{Mix}$ | Energy requirements due to mixing (MJ/d) |
| $b_5$ | Parameter determining degree of correlation between initial body weight and lipid to protein ratio at maturity | $E_N$ | Energy requirements due to increase group size (MJ/d) |
| $b_6$ | Parameter determining degree of correlation between initial body weight and mature protein content | $E_{pg}$ | Energy requirement for potential growth (MJ/d) |
| $b_7$ | Parameter determining degree of correlation between ability to cope with social stressors and initial body weight | $E_{req}$ | Total energy requirement (MJ/d) |
| CPC | Crude protein content of diet (g/kg) | ExH | Extra heat required (MJ/d) |
| $CP_d$ | Crude protein digestibility (kg/kg) | $e_p$ | Efficiency of ideal protein utilisation for growth |
| CVg | Coefficient of variation of genetic variation | $e_p$* | Maximum value of ep |
| | | FCR | Feed conversion ratio, kg feed eaten per kg body gain (kg/kg) |
| | | $FI_a$ | Actual feed intake (kg/d) |
| | | $FI_c$ | Constrained feed intake (kg/d) |
| | | $FI_d$ | Desired feed intake (kg/d) |
| | | $FI_{ds}$ | Desired feed intake of stressed animal (kg/d) |

| | |
|---|---|
| FR | Feeding rate (kg/min) |
| $FR_{max}$ | Maximum feeding rate (kg/min) |
| FSA | Feeder space allowance (feeders/pig) |
| $FSA_{crit}$ | Critical feeder space allowance (feeders/pig) |
| $g_1$ | Scalar relating relative daily gain due to space allowance with potential relative daily gain |
| $g_2$ | Scalar relating relative daily gain due to group size with potential relative daily gain |
| $g_3$ | Scalar relating maximum feeding rate to body weight |
| $g_4$ | Scalar relating relative daily gain due to mixing with potential relative daily gain |
| $g_5$ | Scalar relating relative daily gain due to mixing with potential relative daily gain |
| $HI_{FI}$ | Heat increment of feeding at maintenance (MJ/kg) |
| $HI_L$ | Heat increment of lipid deposition (MJ/kg) |
| $HI_P$ | Heat increment of protein deposition (MJ/kg) |
| $HL_{max}$ | Maximum heat loss (MJ/d) |
| $HL_{min}$ | Minimum heat loss (MJ/d) |
| HP | Heat production (MJ/d) |
| $h^2$ | Heritability |
| IDCP | Ideal digestible crude protein |
| IDCPC | Ideal digestible crude protein content of diet (g/kg) |
| $k_1$ | Scalar determining ash to protein ratio at maturity |
| $k_2$ | Scalar for determining water content of gain |
| L | Whole-body lipid content (kg) |
| $L_m$ | Mature lipid mass (kg) |
| $L_{min}$ | Minimum body lipid content (kg) |
| $L_m/P_m$ | Mature Lipid to Protein ratio (kg/kg) |
| MEC | Metabolisable energy content of diet (MJ/kg) |
| $M_e$ | Constant for calculating $E_{maint}$ |
| N | Pig group size |
| P | Whole-body protein content (kg) |
| $P_g$ | Protein requirement for potential growth (kg/d) |
| $P_{maint}$ | Maintenance protein requirement (kg/d) |
| $P_m$ | Mature protein mass (kg) |
| $P_{req}$ | Total daily protein requirement (kg/d) |
| $p_P$ | Proportion of protein mass in subcutaneous tissue (kg/kg) |
| $p_L$ | Proportion of lipid mass in subcutaneous tissue (kg/kg) |
| Q | Total heat loss (MJ/d) |
| $Q_c$ | Convective heat loss (MJ/d) |
| $Q_e$ | Evaporative heat loss (MJ/d) |
| $Q_f$ | Heat lost through floor (MJ/d) |
| $Q_r$ | Radiative heat loss (MJ/d) |
| $Q_w$ | Heat lost to wet skin (MJ/d) |
| Q | Body weight scalar |
| R | Relative daily gain ($d^{-1}$) |
| RH | Relative Humidity (%) |
| RHP | Required reduction in heat production (MJ/d) |
| $R_f$ | Effective thermal resistance of floor ($^oCm^2/W$) |
| $R_{Mix}$ | Relative daily gain due to mixing (%) |
| $R_N$ | Relative daily gain due to group size (%) |
| $R_p$ | Potential relative daily gain ($d^{-1}$) |
| $R_{SPA}$ | Relative daily gain due space allowance (%) |
| $R_s$ | Relative daily gain of stressed animal ($d^{-1}$) |
| $R_t$ | Tissue thermal resistance ($^oCm^2/W$) |
| SA | Total surface area of pig ($m^2$) |
| SPA | Space allowance ($m^2/BW^{0.67}$) |
| $SPA_{crit}$ | Critical space allowance ($m^2/BW^{0.67}$) |
| $T_a$ | Air temperature ($^oC$) |
| $T_b$ | Body temperature ($^oC$) |
| $T_l$ | Lower critical temperature ($^oC$) |
| $T_s$ | Temperature of pig skin ($^oC$) |
| $T_u$ | Upper critical temperature ($^oC$) |
| t | Time taken to reach final body weight from initial weight (days) |
| v | Biological value of diet |
| W | Whole-body water content (kg) |
| $W_{air}$ | Water content of air (g/kg) |
| WHC | Water holding capacity of diet (kg water/kg dry feed) |
| Wm/Pm | Mature water to protein ratio (kg/kg) |
| w | Exponent for calculating water content of gain |
| $X_h$ | Factor relating $Q_e$ to $W_{air}$ |
| $x_1$ | Scalar relating energy requirements due to group size with maintenance energy requirements |
| $x_2$ | Scalar relating energy requirements due to mixing with maintenance energy requirements |
| $x_3$ | Scalar relating energy requirements due to mixing with maintenance energy requirements |
| $\mu$ | Coefficient relating $e_p$ to MEC and DCPC |
| $\mu B^*$ | Population mean scaled rate parameter |
| $\mu EX$ | Population mean ability to cope with social stressors |
| $\mu L_m/P_m$ | Population mean lipid to protein ratio at maturity (kg/kg) |
| $\mu P_m$ | Population mean mature protein content (kg) |

| | | | |
|---|---|---|---|
| $\sigma B^*$ | Standard deviation of population scaled rate parameter | $\sigma P_m$ | Standard deviation of population mature protein content (kg) |
| $\sigma EX$ | Standard deviation of populations ability to cope with social stressors | $\nu$ | Air velocity (m/sec) |
| $\sigma L_m/P_m$ | Standard deviation of population lipid to protein ratio at maturity (kg/kg) | | |

# General Introduction

The performance of pigs reared commercially is often considerably below that seen under good experimental conditions or in breeding stations. For example, Campbell and Taverner (1985) found growth rate to be 28 % lower in commercial units than in experimental conditions and Black *et al.* (1999) suggested that performance levels of pigs raised in commercial conditions were 70 to 80 % of those observed under 'ideal' conditions. At least some of this decrease in performance can be attributed to factors in the physical, social and infectious environments. These factors are here termed environmental stressors. Quantifying the effects of environmental stressors may allow the removal of those constraints that prevent pigs achieving their potential under farm conditions and substantially increase the profitability of commercial pig enterprises.

The aim of accurately predicting animal growth has led to the development and use of a many animal growth simulation models. They have been developed for the majority of domestic species, including poultry (Emmans, 1981), cattle, (Williams and Jenkins, 2003), sheep (Black, 1974; Blaxter *et al.*, 1980), dairy cows (Baldwin *et al.*, 1987) and pigs (Whittemore and Fawcett, 1976; Black *et al.*, 1986; Moughan *et al.*, 1987; Pomar *et al.*, 1991; Bridges *et al.*, 1992; Ferguson *et al.*, 1994; NRC, 1998; Birkett and de Lange, 2001). By transforming information and concepts into mathematical equations, and translating these into computer programs, a vast store of information can be considered simultaneously in a way that cannot be done by direct experimentation and with an accuracy that would otherwise be impossible to accomplish (Ferguson, 1998). Growth models are of interest and value to both research scientists and industry as a method of assessing and predicting performance of different kinds of animal under a wide range of conditions. Limiting factors within a system can be identified, the consequences of genetic selection predicted and research priorities defined.

Different approaches to pig simulation modelling have been published that have advanced our understanding of pig performance under a wide range of environmental conditions. They range from the first relatively simple attempt to model pig growth developed by Whittemore and Fawcett (1974, 1976), where predictions are based

upon empirical equations, to more recent and elaborate attempts such as those made by Black *et al.* (1986), NRC (1998), Birkett and de Lange, (2001) and Pomar *et al.* (2003). These latter models contain various combinations of empirical and conceptual/mechanistic equations usually with an underlying biological basis. Attempts to predict feed intake, although still not universal, are more frequent in recent modelling attempts (e.g., Black *et al.*, 1986 Bridges *et al.*, 1992; Ferguson *et al.*, 1994) and more factors have been considered and introduced as model inputs. Stressors in the physical environment, such as ambient temperature, humidity, air velocity and floor type have been comprehensively modelled (e.g., Bruce and Clark, 1979; Black *et al.*, 1986). Factors which may act as social stressors, which include mixing, space allowance, group size and feeder space allowance on the other hand, have been largely ignored. This is mainly due to a lack of quantitative data on which to build models and a lack of understanding of how such stressors affect performance. Effects of the infectious environment are yet to be included in animal growth simulation models in a systematic way.

Models intended to simulate pig performance typically represent a single animal (e.g., Whittemore and Fawcett, 1976; Black *et al.*, 1986; Pomar *et al.*, 1991; Bridges *et al.*, 1992). However, due to between-animal variation there may be differences between the response of the average individual and the mean response of the population, which is an average of all individuals (Fisher *et al.*, 1973; Ferguson *et al.*, 1997). In order to attempt to predict adequately the response of a population in a given environment it is necessary to take account of between animal variation (Emmans and Fisher, 1986). Considering between animal variation and the degree of variability around the mean response is essential when models are used to predict nutrient requirements (Fisher *et al*, 1973; Curnow, 1973, 1986), optimise pig production systems (Pomar *et al.*, 2003) and devise animal breeding strategies (Knap, 1995). The stochastic pig growth models of Ferguson *et al.* (1997), Knap (2000a) and Pomar *et al.* (2003) predict the mean population response by taking the average of the simulated individual pig responses. These models deal only with variation in potential growth. Any variation that may exist between individuals in initial state and ability to cope when exposed to environmental stressors is ignored.

Even under the best experimental conditions, there is likely to be variation in initial state between pigs at the start of the trial period and it is expected that variation in ability to cope exist within populations. Group composition and the individual's position within the social hierarchy are likely to affect the ability of an individual to cope in a given social environment.

### *Objectives*

The objective of this thesis was to predict the effect of environmental stressors on the feed intake and performance of growing pigs using simulation modelling. Only physical and social environmental stressors were considered, with infectious stressors assumed to be absent. The response of the 'average' individual and the mean population response were predicted. The model is based at the level of the whole animal. Energy and protein are dealt with in the model to represent the way in which the pig uses these resources to meet its requirements. Because excretion is not considered protein is described only as ideal digestible crude protein and not at the level of the individual amino acids. The aims and corresponding Chapters of this thesis were to:

*Chapter 1:* Choose a suitable predictor of potential pig growth to act as a starting point for model simulation, i.e., to provide an upper limit to growth rate. This upper limit can be termed potential growth and is defined as the maximum rate at which an animal can grow under non-limiting conditions. It is related to the genetic characteristics and current state of the individual animal.

*Chapter 2:* Develop a deterministic, dynamic model to predict the effects of genotype and the nutritional and thermal environments on the voluntary feed intake, growth and body composition of growing pigs.

*Chapter 3:* Test and evaluate the model developed in Chapter two against experimental data from the literature to determine the appropriateness and 'value' of the model.

*Chapter 4:* Quantify the effects of social stressors on the performance of growing pigs, including genetic variation in their ability to cope (EX), and incorporate these relationships into the model developed in Chapter 2. The value of EX adjusts both the intensity of stressor at which the animal becomes effectively stressed, and the extent to which stress reduces performance and increases energy expenditure at a given stressor intensity. The social stressors considered were group size, space allowance, feeder space allowance and the occurrence of mixing.

*Chapter 5:* Extend the model developed in Chapter 4 to create a stochastic population model able to deal with between-animal variation. This allowed the impact of individual variation on the performance of a population to be investigated. Variation between individuals in growth potential, initial state and EX was considered.

*Chapter 6:* Compare the variation predicted by the population model described in Chapter 5 with the phenotypic and genetic variation observed from data from pigs raised under experimental conditions. Three models were simulated to determine to what extent variation in the genetic growth parameters, initial state and EX influenced and contributed to the variation generated in average daily gain and feed intake.

Finally, in the general discussion the main outcomes of this thesis are outlined and four key topics not covered in previous Chapters are then discussed. Firstly, the problem of evaluating models is discussed. Secondly, some limitations of the model developed in this thesis are highlighted and suggestions made on how it may be improved. Thirdly, the problems associated with the estimation of parameter values are discussed with particular reference to EX. Finally, the practical implications of EX in relation to production, welfare and genetic selection are considered.

# Chapter 1

## Describing and predicting potential growth in the pig

*"The use of a growth function to describe data is intended to assist and guide, not replicate experimental analysis. Experimental and mathematical analyses, like other action and thought, are mutually supplementary" (Brody, 1945).*

## 1.1. Abstract

Most animal growth models contain an explicit growth function. It determines the pattern of growth over the lifetime of the animal and defines an upper limit to growth rate (the potential). The criterion of the 'goodness-of-fit' to one or more sets of data is frequently used to select a suitable growth function. Alternative criteria are described here that can be used to choose between forms that describe potential growth. Of the functions reviewed only a few fulfilled all of the proposed criteria. Of these the Logistic and Gompertz functions were favoured because of an economy of parameters and their ability to describe relative growth rate as a simple function of size. The Logistic function was rejected on the grounds of its numerical consequences for growth in pigs over a wide range of degrees of maturity, leaving the Gompertz function to be tested for its ability to make sensible predictions of potential growth. Pre-natal growth data, assumed to occur under non-limiting conditions as long as the mother is not subjected to extremely adverse nutritional conditions or incidence of infection, were used to estimate the values of the two parameters - the growth coefficient and the initial condition - given an estimate of mature size. The values were comparable with literature estimates based on post-natal growth and predictions of growth rate over a wide range of degree of maturity were thus sensible. On these grounds, and because it uses few parameters all with biological meaning, the Gompertz function is proposed as a suitable descriptor of potential growth. Furthermore, it has the added benefit of being able to be used to predict the growth of the individual chemical components of the body, important in animal modelling, by the use of allometry.

## 1.2. Introduction

Growth is an important attribute of organisms and hardly seems to justify any particular formal definition (Lawrence and Fowler, 1997). The simple concept of

growth as an increase in size, which goes back to Aristotle, is preferred to the many more complicated descriptions often proposed.

The pattern of growth from conception to maturity has been the subject of much mathematical analysis with the result that there is a plethora of functional forms that claim to predict growth rates of animals through various stages of life. The aim of predicting animal growth accurately has further led to the development and use of animal growth simulation models, in which growth is predicted under a range of conditions from an array of mathematical equations, logical conditions and rules that can be solved rapidly using computer simulation (e.g. Black *et al.,* 1986; Bridges *et al.,* 1992a and b). The usual starting point for such models is a growth function that sets an upper limit to growth rate at a size. In some cases growth may be made the difference between anabolic and catabolic processes (von Bertallanfy, 1957; Bastianelli and Sauvant, 1997) each described by its own functional form.

Potential growth can be defined as the maximum rate at which an animal can grow under non-limiting conditions. It is related to the genetic characteristics and current state of the individual animal. Among the necessary requirements for non-limiting conditions are: (i) feed must be available *ad libitum*; (ii) nutrient contents must at least meet the required ratios to energy; (iii) intake must not be constrained by the bulk of the feed or the presence of toxins; (iv) environmental factors, such as high temperature and disease, must not constrain intake (Emmans and Kyriazakis, 1999, 2000).

Environmental effects on growth mean that any actual growth may not always equate to potential growth (Whittemore *et al.,* 1988). As it may not be clear that potential growth has been achieved in a given situation, it is important that a growth function predicts potential growth rather than simply describes a particular data set obtained in conditions that may be less than ideal.

In this Chapter I am concerned with the form of potential growth, rather than with the statistical excellence of the fit of a function to measured values of actual growth.

The objective is to describe and defend the criteria used to choose suitable forms of growth function. Having chosen a suitable sub-set these are subjected to simple quantitative evaluation.

## 1.3. Theory

The many functions used in the literature to describe animal growth are examined below to find the most suitable. The criteria used to make the choice are described and discussed first. The functional forms are in Table 1.1.

### *1.3.1. Criteria used*

*1.3.1.1. Fewer parameters are preferred.* The fewer the parameters, the easier the function is to understand and use. There is likely to be less error associated with its use and in the estimation of the values of its parameters. The criterion of preferring a function with fewer to one with more parameters is a version of the long established rule known in science as that of Occam's Razor (Thorburn, 1915). If this rule is not used then a form with (n + 1) parameters will always be preferred to one with n parameters using specious criteria such as increased flexibility. An example is the estimation of rate coefficient(s). One is required by the 3 parameter Logistic function (Robertson, 1908) whereas two are needed in the functions with four parameters, such as those suggested by Bridges *et al.,* (1986) and Richards (1959). It must be easier to estimate one rather than two.

*1.3.1.2. Functions in which the parameters can be given biological meaning are preferred.* The parameters of a growth function should be able to be ascribed biological meaning. This requirement means that the values of the parameters of the function can be attributed to a given kind of pig, rather than being simply a consequence of elaborate mathematics. The changing shape of any growth curve can of course be fitted to data by using a series of parameters, but the more parameters that are used, the more often any relationship with anything recognisable as a biological factor becomes obscure. It may be possible to be flexible in choosing which parameters to specify for a given functional form.

**Table 1.1**: *A list of growth functions and desired criteria for predictors of potential growth. Weight, W, is used as the scale for size throughout*

| Reference: | $W = f(t)$ | No. of parameters | Ability to be expressed as 'rate is a function of state' | Continuous growth | Asymptote | $dW/dt \rightarrow 0$ at $W_o$ and A | Point of inflection | Monotonic decrease in relative growth rate |
|---|---|---|---|---|---|---|---|---|
| Gompertz (1825) | $A.\exp(-\exp(-G_o-(kB.t)))$ | 3 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Robertson (1908) (Logistic) | $(A / (1 + ((A - W_o)/W_o)))(\exp - (A.k.t))$ | 3 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Hill (1913) | $(W_o.k^n + A.t^n) / (k^n + t^n)$ | 3 | x | ✓ | ✓ | x | ✓ | ✓ |
| Brody (1945) $t \leq t^*$ | $W_o.\exp(c.t)$ | 3 | ✓ | x | ✓ | ✓ | ✓ | x |
| $t \geq t^*$ | $A [1 - \exp(-k(t - t^*)]$ | | | | | | | |
| Von Bertalanffy (1957) | $\{n/k - (n/k - W_o^{(1-m)})e^{-(1-m)k.t}\}^{1/(1-m)}$ | 4 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Janoschek (1957) | $A - (A - W_o).\exp(-k.t^p)$ | 4 | x | ✓ | ✓ | ✓ | ✓ | ✓ |
| Richards (1959) | $W_o.A/(W_o^n + (A^n - W_o^n)\exp(-(k.t)))^{1/n}$ | 4 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Parks (1965) | $A.(1 + a.\exp(-b.t) + c.\exp(-d.t))$ | 5 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Moore (1985) | $A.(1 + \exp(-p_n.\log_e(t - 3.5)/A^{0.27}))^{-1/0.27}$ | Varies with $^ap_n$ | x | ✓ | ✓ | ✓ | Varies with $^ap_n$ | Possible |
| Black *et al.*, (1986) | $dw/dt = k((A - W)/A))(W + b)^c$ | 4 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Bridges *et al.* (1986) | $W_o + A.(1 - \exp(-(m.t^a)))$ | 4 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| France *et al.* (1996) | $A - (A - W_o) \exp[-k (t-T) + 2c(\sqrt{t} - \sqrt{T})]$ | 5 | x | ✓ | ✓ | x | ✓ | x |
| Wan *et al.* (1998) | $A - (1 / (b + c.\exp(k.t)))$ | 4 | x | ✓ | ✓ | ✓ | ✓ | ✓ |
| Lopez *et al.* (2000) | $(W_o.k^c + A.t^c) / (k^c + t^c)$ | 4 | x | ✓ | ✓ | x | ✓ | ✓ |
| Exponential polynomials | $\exp(a_0 + a_1t + a_2t^2 + a_3t^3....)$ | Varies with $a_x$ | x | ✓ | x | x | Many | x |

Where in all cases $W_o$ is the initial weight of the animal (kg), A is the animal's mature weight (kg), k is the rate parameter and t is time (days). Other parameters are constants individual to the function.

$^ap_n$ is a polynomial extension

*1.3.1.3. Functions with the ability to be expressed in the 'rate is a function of state' form are preferred.* France and Thornley (1984) stated the rule that 'rate is a function of state' is better than making rate a function of time *per se*. Time is the medium in which size increases. It is well known that actual growth rate may be reduced or even be negative (e.g. Kyriazakis and Emmans, 1991; Stamataris *et al.*, 1991) (Figure 1.1), whereas time flows at a uniform rate (Brody, 1945). The change in size over time is then seen as the result of integrating growth rate at a size with respect to time.

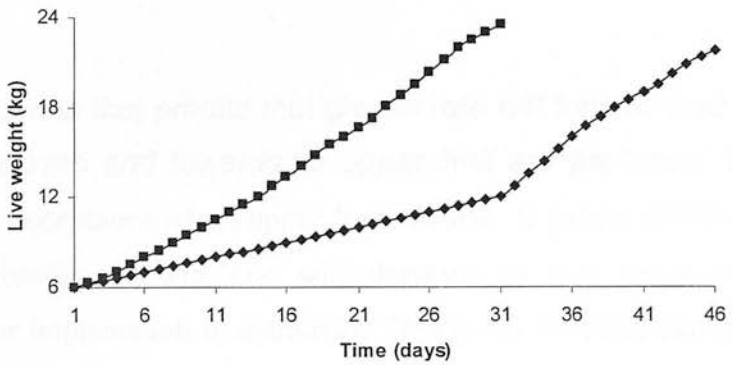


**Figure 1.1.** *Live weight against time for pigs given either ad libitum throughout (■) or restricted access (♦) to the food until 12kg and ad libitum access thereafter. Reproduced from Stamataris et al. (1991).*

*1.3.1.4. Growth should be seen as a continuous process.* It is assumed that potential growth is a continuous process that results in a single, smooth growth curve and a similarly smooth growth rate curve when plotted against size. This is equivalent to saying that the genetic make-up of the animal is the same at all times. The discontinuities of growth that have been claimed to be present in some data sets (e.g. Robertson 1923; Brody, 1945; Gall and Kyle, 1968) may well simply reflect external influences that have not allowed potential growth to be expressed at all times. Multiphase functions (e.g. Koops, 1986; Koops and Grossman, 1991) with their large number of parameters should be used only with considerable caution. Multiple functions may also lead to different estimates of growth rate at a particular weight or age as exemplified by the equations formulated by Brody (1945) as noted by Parks (1982).

*1.3.1.5. Functions with an asymptotic value are preferred.* The assumption that there is no upper limit to the size of an animal would not seem to be reasonable. The assumption of an upper limit to size, however difficult it may be to estimate its value, allows the idea of a degree of maturity to be used (Taylor, 1980). This allows easier comparisons of growth curves between species of with different upper limits to size. Some biologists studying fish growth argue that fish have no upper limit to their size (Bureau *et al.,* 2000). This is not case for mammals and is not the position taken here.

*1.3.1.6. Functions that predict that growth rate will tend to zero as size tends both towards zero and towards its upper limit are preferred.* This follows in part from the acceptance of an upper limit to size. It seems intuitively sensible to assert that absolute growth rate will decrease as size tends towards that at fertilisation, or implantation in mammals. This is not to assert that growth rate will be zero when size is zero. An animal of zero weight does not exist.

*1.3.1.7. Functions that have a size at which growth rate is at a maximum are preferred.* Growth functions should predict a size at which growth rate ceases to increase and starts to decrease. This is a result of the fact an animal has an initial small size and an upper limit to its size. Consequently there is a size at which growth rate will be at a maximum. This is called the point of inflection (POI) and is a direct input in some functions such as those devised by Brody (1945) and shown in Table 1.1. In this function the time at which growth rate is at a maximum is sometimes said to represent sexual maturity. In some functions the POI occurs at a fixed degree of maturity. Others, with greater flexibility allow the POI to occur at any stage of maturity by the addition of one, or more, further parameters (e.g. Von Bertalanffy, 1957; Janoschek, 1957; Richards, 1959; Moore, 1985; Black *et al.,* 1986; Bridges *et al.,* 1986; France *et al.,* 1996; Wan *et al.,* 1998; Lopez *et al.,* 2000).

*1.3.1.8. Functions that predict that relative growth rate will decrease continuously towards zero, as size increases are preferred.* The rate at which

the animal grows relative to its current size, S, is R = (dS/dt)/S and is an important variable. A simple relationship between R and S is preferred. A reasonable assumption is that R will decrease monotonically as S increases (Emmans and Kyriazakis, 1999). Two functions, Table 1.1, showing a desirable R versus S relationship are the Logistic (Robertson, 1908), which describes a linear decrease in R as S increases, and the Gompertz (1825), which predicts a linear decrease in R as the logarithm of S increases (Figure 1.2). The functions of Richards (1959) and Bridges (Bridges *et al.,* 1986), with one more parameter, are also able to display these particular relationships as special cases, Table 1.1.

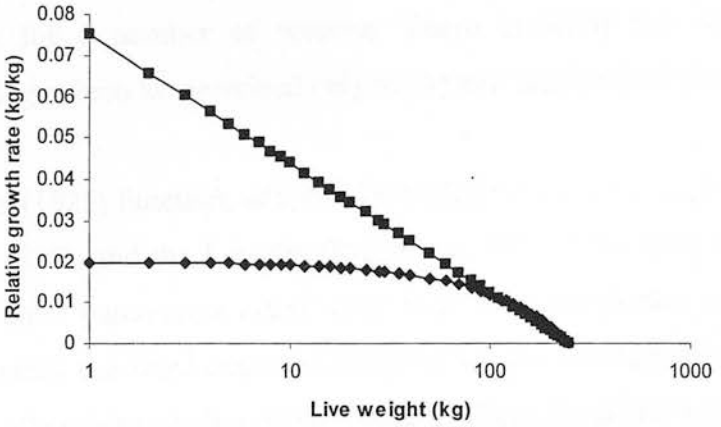


**Figure 1.2**. *The relationship between relative growth rate and live weight on a logarithmic scale predicted by the Logistic (♦) and Gompertz (■) functions.*

*1.3.1.9. The quantitative predictions of the function, with realistic parameter estimates, should predict growth rates that are biologically realistic.* Although perfect agreement with any one or more real data sets is not necessary it is important that the function chosen can describe all stages of growth in a quantitative way that is biologically sensible. Whether the predictions of a function are seen as sensible will inevitably be a matter of judgement, to at least some extent.

### *1.3.2. Assessment of possible functions*

From the growth functions identified in a diligent search of the literature, only a few were found to fulfil all the necessary criteria (Table 1.1). These are the Gompertz (1825), Logistic (Robertson, 1908), von Bertalanffy (1957), Richards (1959), Black

(Black *et al.,* 1986) and Bridges (Bridges *et al.,* 1986) functions. The function of Chanter (1976), given by France and Thornley (1984), was not used as it was seen as having no advantage over the Richards function. Although the function of Parks (1965) also fulfils the listed criteria it is not considered any further in the selection of a suitable growth function as it includes feed intake as one of its parameters. Feed intake is better seen as a consequence of potential growth rather than as a cause of it (Emmans, 1997; Emmans and Kyriazakis, 2001). The Brody 'function' (1945) failed to meet the criterion of describing continuous growth as it was in fact two equations. The functions of Janoschek (1957), Moore, (1985), France *et al.* (1996), Wan *et al.* 1998, Lopez *et al.* (2000) and the exponential polynomials, all failed to meet the listed criteria for a number of reasons. These included the shared failure of apparently being able to be described only as explicit functions of time.

The Gompertz (1825) function, adopted for biological phenomena by Wright (1926) and Courtis (1937), and the Logistic (Robertson, 1908) both have the advantage of having only three parameters rather than four. A consequence is that maximum growth rate occurs at a fixed degree of maturity. On the criterion of fewer parameters being better, other things being equal, either of these functions will be preferred if they are able to describe potential growth suitably well. If neither is successful then the functions with four parameters will need to be assessed.

An important property of a growth function is the relationship it proposes between R and S as it is this that determines the growth rate at any particular degree of maturity. The Gompertz (1825) and Logistic (Robertson, 1908) functions both have the desirable property of making R a simple function of S. If R decreases linearly with S then the Logistic (Robertson, 1908) function results. If R decreases linearly with the logarithm of S then we have the Gompertz (1825) function. An example is shown in Figure 1.2. A linear relationship means that the two key parameters (an initial state parameter is the third) of the function can be deduced from only two data points, although accuracy will be improved by including more (Ferguson and Gous 1993a).

The Logistic function (Robertson, 1908) can be rejected, at least for pig growth, because of the numerical consequences of the relationship it proposes between the relative growth rate and size. The linear decrease in R as S increases leads to a maximum growth rate at 0.5 maturity and has the consequence that growth rate changes in a symmetrical way around this degree of maturity. The change in growth rate above half maturity exactly mirrors that below. Consequently growth rate is predicted to be either implausibly slow during early life or implausibly fast during later life, as will be shown.

Using weight, W, as a measure of size we can consider a pig with an upper limit to its size, (A), of 250 kg, a birth weight ($W_o$) of 1.5 kg and a maximum growth rate (dW/dt) of 1.25kg/d. From these plausible values the value of the Logistic growth rate parameter, k, is estimated as 0.00008 $d^{-1}$. The equations of the Logistic function are:

$$W = (A /(1 + ((A - W_o)/W_o)))(\exp-(A.k.t)) \quad (1.1)$$

$$dW/dt = k.W(A - W) \quad (1.2)$$

It is then predicted that a pig will take 92 days to get to the expected weaning weight of 9.0 kg. The value of k needs to be increased by a factor of more than three, to 0.00026 $d^{-1}$, to allow a realistic prediction of a weight of 9.0 kg at 28 days from birth. However, with this value the maximum growth rate, which will be attained at 125 kg = 0.5A, is predicted to be 4.06 kg/d, a value that can only be seen as totally unrealistic.

The assumption that the decrease in relative growth rate as the logarithm of size increases is linear, as predicted by the Gompertz (1825) function, does not lead to such problems. The maximum growth rate is predicted to occur at A/e. Using the same values as were used to 'test' the Logistic equation (A = 250 kg, a birth weight ($W_0$) of 1.5 kg and a maximum growth rate of 1.25 kg/day), the value of the growth rate parameter, B, is estimated as B = 0.0136 $d^{-1}$. The equations are:

$$W = A.(\exp(-\exp(-G_o - (B.t)))) \quad (1.3)$$

$$dW/dt = B.W.\log_e (A/W) \quad (1.4)$$

where $G_o = -\ln(-\ln(W_0/A))$ is a transformed initial degree of maturity at t = 0, taken here to be at birth. With these values the pig is predicted to reach a weight of 9.0 kg at 32 days from birth. Although the two functions may appear to be superficially similar (Figure 1.3) they have the consequence of a three-fold difference in the prediction of the time needed to go from 1.5 to 9.0 kg. This quasi-quantitative test shows that the Gompertz form leads to a much more acceptable prediction than does the Logistic.

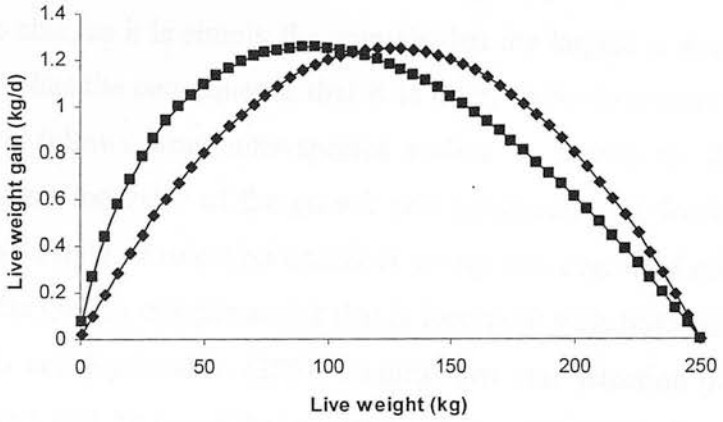


**Figure 1.3.** *The relationship between daily live weight gain and live weight predicted by the Logistic (♦) and Gompertz (■) functions.*

The pattern of growth described by the Gompertz (1825) function is simple and appears sensible. Nevertheless, many authors believe that the assumption that maximum growth rate occurs at a fixed proportion of maturity, an inevitable consequence of using a three parameter function, is a disadvantage (e.g. Bastianelli and Sauvant, 1997; Schinckel, 1999). 'If it were shown that the inflexion point and adult body weight were not associated, then it would be necessary to choose a function with an extra parameter, thus allowing a variable POI to be determined' (Bastianelli and Sauvant, 1997). There has also been some debate about the effect that genetic selection may have on the degree of maturity at which the POI occurs (see Knap, 2000). However, as Emmans and Kyriazakis (2001) state, 'a more fruitful

debate would be about the effects of selection (genetic) on the underlying relationship between R and S, as it is this relationship that leads through algebra rather than biology to the absolute growth rate and relative growth rate'. It is important to know if the form of the relationship between R and S is likely to be changed by genetic selection. If this is the case then a function with three parameters, and consequently a fixed POI and fixed relationship between R and S, would not be a suitable descriptor of potential growth.

Genetic selection for an increased growth rate by selecting for an increased weight at a particular age, seems likely to have two effects (Emmans and Kyriazakis, 2000; Knap, 2000). Firstly, selection for size at a very high degree of maturity will mainly increase mature size, as it is simply the animals that are largest at maturity that will be selected. This has the consequence that R is likely to be increased at all weights. This expectation follows from inter-species scaling as shown by Taylor, (1980), which also suggests the value of the growth rate parameter will decrease as mature size increases. Secondly, if selection occurs at a very low degree of maturity, then it will be mainly the growth rate parameter that is increased with little effect on mature weight. Emmans and Kyriazakis, (2001) suggest that real selection programmes in commercial stocks will be somewhere between these two levels. It seems unlikely that the form of the relationship between R and S will change as selection proceeds, although the values of the parameters will. This is equivalent to stating that there is no genetic variation in the form of the function but only in the values of its parameters.

If there is a change in the form of the growth function under selection then the Richards (1959) function, with four parameters can be used. It is able to mimic the Gompertz (1825) function when the value of its fourth parameter (n) is equal to zero. The equations are:

$$W = W_o.A/[W_o^n + (A^n - W_o^n).e^{-kt}]^{1/n} \quad (1.5)$$

$$dW/dt = k.W(A^n - W^n)/n.A^n \quad (1.6)$$

where k is the rate parameter and n is a parameter able to vary between –1 and 1.

## 1.4. Quantitative tests of the proposed function

To test a functional form for its ability to describe potential growth, against a set of data, it is necessary to assume that the data set in question is representative of growth in non-limiting conditions. Pre-natal growth occurs within the body of the mother and it can be assumed that, as long as the mother is not subjected to extremely adverse nutritional conditions or incidence of infection, that conditions in which pre-natal growth occur are non-limiting (Coop and Kyriazakis, 1999; Robinson *et al.*, 1999). In the final stages of pregnancy uterine capacity may inhibit potential foetal growth due to space limitation (Van Oijen *et al.* 1993).

*1.4.1. Parameter estimation.* Pre-natal weight data were obtained by slaughtering Landrace x Large White sows at 30, 45, 65 and 100 days after conception (C.Ashworth, unpublished results, given in Table 1.2.). The sows were maintained under usual husbandry conditions (i.e. no extreme treatments were imposed). The data were used to estimate the values of the parameters of the Gompertz function, B and $G_o$, given the *a priori* estimate for A of 250 kg (Knap, 2000). As expected (Emmans, 1997) choosing values of A between 125 and 500 kg had little effect on the values of the parameters estimated.

**Table 1.2.** *Pre-natal growth results*[a]

| Day of Pregnancy | Number of sows | Total number of foetuses | Average foetus weight (g) | [b]Degree of maturity |
|---|---|---|---|---|
| 30 | 3 | 32 | 1.48 | 0.000006 |
| 45 | 5 | 62 | 19.61 | 0.000078 |
| 65 | 3 | 37 | 173.43 | 0.000694 |
| 100 | 5 | 54 | 888.17 | 0.003533 |

[a]compiled from data supplied by C.Ashworth

[a]If a mature weight of 250kg is assumed.

The values of the Gompertz variable, $G_t$, as defined by equation (1.7), at each of the four stages of pregnancy were estimated and the values regressed on metabolic age, T, (Equation 1.8), to estimate the values of $G_0$ and B* (Figure 1.4).

$$G_t = -\ln(-\ln(W/A)) \quad (1.7)$$

$$T = (t - 3.5)/A^{0.27} \quad (1.8)$$

Where W is the weight of the foetus (kg) at metabolic time T and t is the time (days) from conception.

The regression was:

$$G_t = -2.712 + 0.0472T \qquad r^2 = 0.965 \quad (1.9)$$

The estimates for $G_0$ and B* are -2.712 (s.e. 0.0446) and 0.0472 $d^{-1}$ (s.e. 0.00318) respectively. The value for B* is in good agreement with those estimated by Whittemore *et al.* (1988) of 0.0440 $d^{-1}$ and Knap (2000) of 0.0471 $d^{-1}$. Emmans (1997) estimated a value of 0.0360 $d^{-1}$ from the pre-natal data of Taylor (1980) for eight species of mammal. Values for $G_0$ of –2.504 for the pig data of Taylor (1980) and –2.808 for the combined sheep and cattle data of ARC (1980) were reported by Emmans (1997).

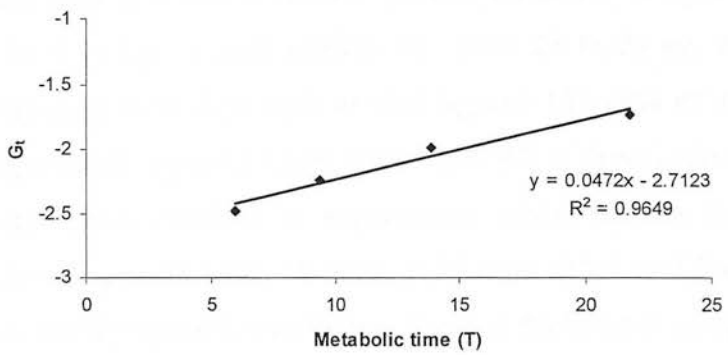


**Figure 1.4.** *Regression of metabolic time, $T = (t - 3.5)/A^{0.27}$, against the Gompertz variable, $G_t = -\ln(-\ln(W/A))$, where t is time (days) W is the current mass (kg) and A is the mass at maturity (kg). The line is the regression G = -2.7123 + 0.0472T.*

Using Taylor's (1980) scaling rule the scaled rate parameter, B*, can be converted to the non-scaled rate parameter, B, through the mature liveweight of the animal.

$$B = B^*/A^{0.27} \quad (1.10)$$

From equation (1.10) the value of B is 0.0106 $d^{-1}$ (s.e. 0.000717). This estimate of B, associated with an *a priori* estimate of A of 250 kg, was obtained from data where the weights were between 0.000006 and 0.0035 of the upper limit to weight.

Over quite different ranges of degrees of maturity other estimates of the value of B for pigs are in very close agreement. Whittemore *et al.* (1988) reported B values of 0.0100 $d^{-1}$ for castrates and females and 0.0110 $d^{-1}$ for entire males. A value of 0.0113 $d^{-1}$ was estimated by Ferguson and Gous (1993a) from the data of Campbell and Traverner (1988) and a value of 0.0093 $d^{-1}$ was estimated by Emmans (1989) for the pigs of Doornenbal (1971, 1972a,b). The B values obtained by Whittemore *et al.* (1988) were from measurements on pigs between 20 and 200 kg whilst the value reported for the pigs of Doornenbal (1971, 1972a,b) were from pigs weighing between 10 and 133 kg.

*1.4.2.Predictions of growth rates.* The values of B and $G_0$ estimated from the pre-natal data were used to estimate various growth variables. Weight at 28 days was estimated to be 9.93 kg, average growth rate from 25 to 90 kg, to be 0.85 kg/d, maximum daily gain to be 0.98 kg/d at 90.8 kg and 137 days of age and age at a slaughter weight of 100 kg as 147 days from birth. All of these estimates are sensible and agree with values obtained in experiments where authors took measures to provide 'non-limiting conditions'. Weights at 28 days of 7.4 to 9.3 kg were reported by Whittemore (1998) and of 8.6 kg by van Erp-van der kooij *et al.* (2000). Palmer *et al.* (1993) reported average daily gains of 1.1 kg/d over the weight rage of 25 to 118 kg. Whittemore *et al.* (1988) estimated time at maximal daily gain to be between 141 and 182 days and age at slaughter at the slightly heavier weight of 104.5kg was reported to be 145 days by Schinckel and de Lange (1996).

## 1.5. Discussion

Most growth models use a growth function as the starting point. The function chosen will determine the pattern of growth over the lifetime of the animal. It will also set

the upper limit to growth rate, the potential, from which actual growth will be predicted given the actual conditions (Whittemore and Fawcett, 1976; Black *et al*, 1986; Ferguson *et al*, 1994).

Many forms of growth function have been used in pig growth models. Whittemore and Fawcett (1976) made the potential growth rate of protein constant over the weight range of 20 to 120 kg. More complex, and hence more flexible, functions were used by Black *et al.* (1986, 1995), Bridges *et al.* (1992a) and Pomar *et al.* (1991). The simplicity of using a single constant as a sufficient description of potential pig growth is more apparent than real. It can apply, if at all, only to a narrow range of degree of maturity and it is surprising that this notion has continued to be used (e.g. de Lange, 1995; Moughan, 1995). On the other hand, highly flexible functions that have many parameters, although popular, often lead to difficulties in the estimation of the values of the parameters that describe a particular genotype of pig (Knap, 2000). Very detailed and complicated experiments would need to be conducted in order to obtain estimates of these parameters (Ferguson and Gous, 1993a), even if the functions applied and non-limiting conditions could be achieved. Convergence, especially when good initial parameter values are not available, may be difficult to obtain (Schinckel and de Lange, 1996) and the global maximum likelihood solution may be hard to identify (Fitzhugh, 1976).

Using a function, which makes biological sense, has much more to recommend it than a search for one that will provide only a close mathematical fit (e.g. Moore 1985) to some particular data. Goodness-of-fit alone is no justification for adopting a given function since several functions may fit the data equally well (e.g. Wan *et al.*, 1998) and it is often unclear how goodness-of-fit should be measured in a number of situations (Kowalski and Guire, 1974). In some cases a formal statistical comparison may be able to be made to test whether a model with a fourth parameter improves the fit over one with only three. An example is that given by Schnute (1981) where the Richards function was found to give no significant improvement over the Gompertz function to some data on the growth of fish.

It is not sensible to expect data on actual growth, which may well depart from the potential because of deficiencies in feeding, environment and health, to be totally consistent with any particular form of growth function (Lewis *et al.,* 2002). Despite this being obvious the literature is full of examples where actual growth data, often of doubtful provenance, have been used to choose between growth functions. Some authors even choose suitable functions on the grounds that they 'must be flexible to fit any commercially achieved pattern of growth' (Schinckel, 1994). Of course choosing more flexible functions by increasing the number of parameters will allow any pattern of growth to be described, but this is not the purpose of a function intended to predict potential growth and to be used in a simulation model. While a number of functions may describe equally well given data sets of growth, the Gompertz function appears most suitable to predict potential growth. It was found that sensible predictions could be made up to close to the upper limit to size using values of the parameters estimated from pre-natal growth data. Weights in the pre-natal set used ranged only between 0.0015 and 0.888 1kg but could be used to predict growth rate at 90 kg and other aspects of post-natal growth performance.

Apart from the advantages of using few parameters (only two plus an initial condition) all with biological meaning and the ability to predict potential growth sensibly, there is a further important consequence of using the Gompertz function. Two assumptions about each of the four chemical components of the body, protein, lipid, ash and water, allow their potential growth to be described by the use of allometric relationships between the chemical components (Emmans, 1987, 1988; Emmans and Kyriazakis, 1999). This appears to be a property that is unique to the Gompertz function (Winsor, 1932).

It is concluded that the Gompertz function is suitable as a descriptor of potential growth in non-limiting conditions. It uses few parameters and holds over a very wide range of degree of maturity. The values of its parameters for a particular kind of pig, or other animal, can be estimated quite simply from data obtained under conditions that at least approximate to being non-limiting. This has been done for pigs by Ferguson and Gous (1993a and b) and Knap (2000). The cases of other species have

been addressed elsewhere (Emmans, 1989, 1997). Once the values of the parameters of the function have been estimated for a given kind of pig then it can be used as the first step towards solving the more difficult problem of predicting actual pig performance in real conditions.

# Chapter 2

## Modelling the effects of the thermal environment and dietary composition on pig performance: model logic and concepts

## 2.1. Abstract

A deterministic, dynamic pig growth model is described that predicts the effects of genotype, the thermal and nutritional environments on feed intake, growth and body composition of growing pigs. From the daily potential for protein gain, as determined by pig genotype and current state, the potential gains of the other chemical components, including 'desired' lipid gain, are calculated. Unconstrained voluntary feed intake is predicted from the current protein and lipid contents of the pig, and the composition of the feed, as that which is needed to permit potential growth to be achieved. The model allows compensatory lipid gain. The composition of the feed is described in terms of its digestible energy content (DEC), ideal digestible crude protein content (IDCPC) and bulkiness. Both energy and protein can be limiting resources and the bulk of the feed may constrain intake. The animal's capacity for bulk is a function of its size. The thermal environment is described by the ambient temperature, wind speed, floor type and humidity and sets the maximum ($HL_{max}$) and minimum ($HL_{min}$) values possible for heat loss. A comparison with heat production (HP) determines whether the environment is hot ($HP > HL_{max}$), cold ($HP < HL_{min}$) or thermoneutral ($HL_{min} < HP < HL_{max}$). A constraint on intake operates in hot environments, while in cold environments, there is an extra thermal demand. If conditions are thermoneutral no further action is taken. Daily gains of each of the chemical components are calculated by partitioning energy intake between protein and lipid gains according only to the energy to protein ratio of the feed. The model builds on others in the literature as it allows predictions on how changes in: (i) the kind of pig; (ii) the animal's current state, which is particularly relevant in cases of compensatory growth; (iii) the dietary composition, and; (iv) the climatic environment, affect feed intake and growth, whilst maintaining simplicity and flexibility.

## 2.2. Introduction

The simulation of animal growth potentially provides a way of predicting animal performance over a wide range of conditions with an accuracy that would otherwise be impossible to accomplish (Ferguson, 1998). Limiting factors within a system can

be identified, the consequences of genetic selection predicted and areas needing further research highlighted. For sensible predictions to be made a sufficient understanding of the animals' response to differences in environmental conditions is needed. Any model simulating animal performance must include an adequate description of the type of animal, it's feeding, and the environment it lives in and be able to predict the interactions between these components.

Different approaches to pig simulation modelling have been published (Whittemore and Fawcett, 1976; Black *et al.*, 1986; Moughan *et al.*, 1987; Pomar *et al.*, 1991; Bridges *et al.*, 1992a and b; Ferguson *et al.*, 1994; National Research Council, 1998; Birkett and de Lange, 2001a and b). Amongst their shortcomings are the failure to predict feed intake, insufficient or very complex descriptions of the pig which makes parameter estimation difficult, unclear rules for partitioning energy between protein and lipid growth, and inadequate descriptions of the thermal and nutritional environments.

The aim here is to build on these approaches to describe a deterministic model that will predict dynamically the effects of genotype, and the nutritional and thermal environments on the voluntary feed intake, growth and body composition of pigs. The starting point is the prediction of potential growth from descriptions of the genotype and current state of the pig. The effects of the thermal and nutritional environments, and interactions between them, on pig performance are then represented.

## 2.3. Materials and methods

### *2.3.1. Assumptions*

The key assumptions in the model are: (i) the animal will always aim to achieve its potential growth, (including compensatory lipid gain), which is dependent only upon its genotype and current state; (ii) voluntary feed intake will always be sufficient to achieve potential growth providing only that it is within the constraints of gut capacity and heat balance; (iii) the animal has free access to a feed that is free of toxins, and, (iv) the animal is in good health and free from disease and infection

throughout. The deterministic model that follows from these assumptions is used to predict the response of a single animal representing the mean of the genotype being simulated. The programming language DELPHI (Borland, 1999), is used to facilitate model operation through a user-friendly visual interface.

### 2.3.2. Description of the model

A key to the notation used throughout the text is shown in the list of abbreviations, whilst the inputs to, and outputs from, the model are listed in Table 2.1.

**Table 2.1.** *Model inputs and main model outputs*

| INPUTS | OUTPUTS |
|---|---|
| Start weight (BW, kg) | Final Body Composition |
| End weight (kg) | Protein (P, kg) |
| Pig Description | Lipid (L, kg) |
| Growth rate parameter (B, /day) | Water (W, kg) |
| Mature protein mass ($P_m$, kg) | Ash (A, kg) |
| Mature lipid to protein ratio ($L_m/P_m$) | Backfat (BF, mm) |
| Feed Composition | Growth (average daily gains) |
| Digestible energy content (DE, MJ/kg) | Protein (dP/dt, kg/d) |
| Crude protein content (CPC, g/kg) | Lipid (dL/dt, kg/d) |
| Crude protein digestibility ($CP_d$, kg/kg) | Water (dW/dt, kg/d) |
| Biological value (v) | Ash (dA/dt, kg/d) |
| Dry matter content (DM, kg/kg) | Empty body (dEBW/dt, kg/d) |
| Water holding capacity (kg water/kg dry feed) | Total body (dBW/dt, kg/d) |
| Environmental Descriptors | Potential daily gains of chemical components |
| Ambient temperature ($T_a$, °C) | Intake |
| Relative humidity (RH, %) | Average daily feed intake ($FI_a$, kg/d) |
| Air velocity (v, m/sec) | Average daily desired feed intake ($FI_d$ kg/d) |
| Floor type | Feed conversion ratio (FCR, kg feed/kg gain) |
| Group size (N) | Heat Production (HP, MJ/d) |
| | Upper critical temperature ($T_u$, °C) |
| | Lower critical temperature ($T_l$, °C) |

#### 2.3.2.1. Unconstrained growth and intake

*2.3.2.1.1. Initial body composition.* The chemical composition of the pig at the start of the simulation period is calculated from the initial body weight (BW, kg),

assuming that the pig has its desired chemical composition. The weights (kg) of ash (A), water (W) and lipid (L) are calculated from P using allometric equations (Emmans and Fisher, 1986; Emmans and Kyriazakis, 1997).

$$A = k_1 P^a \quad \text{kg} \quad (2.1)$$

$$W = k_2 P^w \quad \text{kg} \quad (2.2)$$

$$L = L_m (P^d / P_m^d) \quad \text{kg} \quad (2.3)$$

The values of a = 1 and $k_1$ = 0.19 are assumed to be constant across genotypes (Emmans and Kyriazakis 1997). The value of the scalar $k_2$ is assumed to vary with the weight of protein at maturity, ($P_m$, kg) and is estimated as $k_2 = (W_m/P_m).(P_m^{1-w})$, where $W_m/P_m$ is the water to protein ratio at maturity with an assumed value of 3.04 kg/kg for all genotypes (Emmans and Kyriazakis 1995). The value of w is taken to be 0.855 (Kotarbinska, 1969; Emmans and Kyriazakis, 1995). $L_m$ is the weight of lipid at maturity (kg) and is calculated as $P_m$ multiplied by the ratio of lipid to protein in the mature animal, $L_m/P_m$. The value of d is estimated as $d = 1.46.(L_m/P_m)^{0.23}$ (Emmans, 1997) to reflect its strong relationship with mature fatness.

The value of P at the start of the simulation is calculated for a pig of a given genotype is calculated from the initial BW using the Newton-Raphson iteration method (Stewart, 1986). The genotype defines the values of $P_m$ and $L_m$. The method uses an iterative process to approach the root of a function from an arbitrarily chosen x-value. The estimated value of the root, $x_n$, approaches the real value of x as the number of iterations, n, increases. The equation used is:

$$P_{n+1} = P_n - ((P_n + k_1 P_n + k_2 P_n^w + L_m.(P_n^d/P_m^d) - EBW)/(1 + k_1 + w.k_2.P_n^{w-1} + L_m/P_m^d.P_n^{d-1})) \quad (2.4)$$

When n = 1, the value for $P_n$ is that chosen for P at the start. $P_{n+1}$ represents the next P value and EBW is the empty body weight of the pig (kg). EBW is calculated as 0.95BW to allow for gut fill (Moughan *et al.*, 1987). In trial simulations it was found

that P was calculated to within 0.00001 kg of the true value using no more than six iterations and this value for n was then used throughout.

*2.3.2.1.2. Prediction of potential growth.* The first step in predicting pig performance is to predict the upper limit to the growth of each of the body constituents – the potential growth. The Gompertz growth function was found to be a suitable function to describe potential growth in Chapter 1 and has been used by others (e.g., Emmans, 1988; Emmans and Kyriazakis, 1999 and 2001; Knap *et al.*, 2002). It is used here:

$$(dP/dt)_{max} = P.B \log_e(P_m/P) \quad \text{kg/d} \quad (2.5)$$

$$(dA/dt)_{max} = k_1.(dP/dt)_{max} \quad \text{kg/d} \quad (2.6)$$

$$(dW/dt)_{max} = (dP/dt)_{max}.(W_m/P_m).w.(P/P_m)^{w-1} \quad \text{kg/d} \quad (2.7)$$

The values are the potential daily rates of gain. B is the Gompertz rate parameter, which is dependent upon the genotype of the pig. Lipid gain appears not to have an easily defined upper or potential limit (Emmans and Kyriazakis, 1999) and so it is the 'desired' level of lipid deposition, $(dL/dt)_{des}$ that is calculated as:

$$(dL/dt)_{des} = (dP/dt)_{max}.(L_m/P_m).d.(P/P_m)^{d-1} \quad \text{kg/d} \quad (2.8)$$

Where the actual weight of lipid L differs from that desired (Eq 2.3), the rate at which the pig is predicted to be trying to gain lipid includes correcting any excess or deficit as described below.

*2.3.2.1.3. Energy requirements.* The effective energy system (Emmans, 1994a) is used to calculate the energy requirement. The effective energy content (EEC, MJ/kg) of a diet is the difference between the digestible energy content (DEC, MJ/kg), used as model input, and losses resulting from eating the diet. Losses from fermentation are considered negligible. Although the net energy and effective energy systems are fundamentally different, both systems can be used successfully in mathematical models to predict the metabolic utilisation of feed energy (Rivest *et al.*, 1996). To

calculate the EEC of a diet, the metabolisable energy content (MEC corrected to zero N retention, MJ/kg) of the feed is estimated from DEC and the crude protein content, (CPC, g/kg). This value is then used to calculate the EEC from the chemical composition of the feed.

$$MEC = DEC - 5.63.(CPC/1000) \quad \text{MJ ME/kg} \quad (2.9)$$

$$EEC = 1.17MEC - 4.29.(CPC/1000) - 2.4 \quad \text{MJ EE/kg} \quad (2.10)$$

Maintenance energy requirement ($E_{maint}$, MJ/d) is defined, as that needed to maintain zero rates of retention of both protein and lipid. Energy expenditure from exposure to disease-causing organisms is assumed to be zero and any costs of thermoregulation are calculated separately. Although physical activity may represent a major source of variation in $E_{maint}$ between genotypes (van Milgen *et al.,* 1998), the energy needed for activity is currently included in the estimate for $E_{maint}$ as a fixed cost. The equation devised by Emmans and Fisher (1986) is used to predict $E_{maint}$ as:

$$E_{maint} = M_e.P/P_m^{0.27} \quad \text{MJ/d} \quad (2.11)$$

the value of $M_e = 1.63$ is assumed to be constant across animals and diets, providing that the level of physical activity is constant.

The energy needed above maintenance to allow potential growth to be attained, ($E_{pg}$, MJ/d) is calculated from $(dP/dt)_{max}$ and $(dL/dt)_{des}$. The costs of protein ($b_p$, MJ/kg) and lipid ($b_l$, MJ/kg) retention are assumed to be constant when expressed as EE, and have values of 50 and 56 MJ/kg respectively, providing $(dL/dt)_{des}$ is positive (Emmans, 1994a). The case of negative lipid retention is described later.

$$E_{pg} = b_l.(dL/dt)_{des} + b_p.(dP/dt)_{max} \quad \text{MJ EE/d} \quad (2.12)$$

The total energy requirement ($E_{req}$, MJ/d), assuming thermoneutrality, is the sum of equations 2.11 and 2.12.

*2.3.2.1.4. Protein requirements.* The protein scale used is ideal digestible crude protein, IDCP. The IDCP content of the diet IDCPC (g/kg) is calculated from the crude protein content (CPC, g/kg), multiplied by its digestibility, ($CP_d$, kg/kg) and biological value, (v). The value of the dietary protein, v, is calculated as its proportion of the first limiting amino acid relative to that in a reference protein (Wang and Fuller, 1989). It is close to that of the protein of the whole body (Agricultural Research Council, 1981). Using v as a measure of the value of the protein allows any of the essential amino acids to be limiting.

The form of the equation used for the estimation of $E_{maint}$ is also used to estimate the ideal protein required for maintenance ($P_{maint}$, kg/d):

$$P_{maint} = 0.004.P/P_m^{0.27} \quad \text{kg/d} \qquad (2.13)$$

This equation allows for the comparison of genotypes with differing levels of fatness, by relating $P_{maint}$ to the current and mature protein mass of the pig rather than to BW alone. It is assumed that the efficiency of ideal protein utilisation for maintenance is equal to one (Wang and Fuller, 1989; Ferguson *et al.*, 1994).

The amount of ideal protein needed for potential growth ($P_g$ kg/d) is equal to the potential protein retention divided by the net material efficiency of using ideal protein for protein retention, $e_p$.

$$P_g = (dP/dt)_{max} / e_p \quad \text{kg/d} \qquad (2.14)$$

Following Kyriazakis and Emmans (1992a and b), $e_p$ is made directly proportional to the ratio of MEC to digestible crude protein content (DCPC, g/kg) of the feed up to a critical value (72.55 MJ/kg) at which it becomes maximal, $e_p$*. The value of 0.814 proposed for $e_p$* by Kyriazakis and Emmans (1992a and b) is used here. For diets with MEC/DCPC < 72.55 MJ/kg, $e_p$ is calculated as:

$$e_p = \mu \, (MEC / DCPC) \qquad (2.15)$$

the parameter $\mu$ has a value of 0.0112 and is assumed to be constant across genotypes (Kyriazakis and Emmans, 1992a and b). The total daily protein requirement ($P_{req}$, kg IDCP/d) is the sum of $P_{maint}$ and $P_g$ (Eq. 2.13 and 2.14).

*2.3.2.1.5. Desired feed intake.* It is assumed that the pig will attempt to consume an amount of feed that will satisfy its requirements for both energy and protein (Emmans and Kyriazakis, 1997). The assumption that animals in general 'eat for energy' has wide support (e.g. Bridges *et al.*, 1992; Schinckel and de Lange, 1996; NRC, 1998; Schinckel, 1999). The additional assumption made here that they also 'eat for protein' is less widely made. There is evidence that intake can increase as the protein content falls in pigs (Kyriazakis and Emmans 1992c, Ferguson *et al.*, 2000 a and b) and in other animals (e.g., poultry, Burnham *et al.*, 1992). Whether this effect is seen depends both on the conditions of the experiment and on the way in which the data are analysed (Kyriazakis *et al* 1991a). The feed intake that allows the requirement for both energy and protein for potential growth to be achieved is the 'desired' feed intake ($FI_d$, kg/d). If energy is first limiting, then $FI_d$ will be:

$$FI_d = E_{req}/EEC \quad \text{kg/d} \qquad (2.16)$$

If the feed is first limiting in ideal protein, then $FI_d$ will be:

$$FI_d = P_{req}/IDCPC \quad \text{kg/d} \qquad (2.17)$$

When a feed is perfectly balanced in its energy and protein content, then equations (2.16) and (2.17) will be equal.

### 2.3.2.2. Growth and intake under constrained conditions

*2.3.2.2.1. Dietary constraints on feed intake.* It is assumed within the model that the only dietary constraint imposed upon $FI_d$ is feed bulk. Other dietary constraints that may be present in reality, such as toxins, are ignored. The concept of using a bulk constraint to limit intake is preferred over other approaches that impose a fixed

maximum dry matter intake depending solely on BW, e.g., Whittemore (1983) and Black *et al.* (1986). In the model the scale of bulk is the water holding capacity (WHC, kg water/kg dry feed) devised by Kyriazakis and Emmans (1995). The constrained feed intake ($FI_c$, kg/d) is given by:

$$FI_c = C_{WHC} / WHC \quad \text{kg DM/day} \quad (2.18)$$

$C_{WHC}$ is the animal's capacity for water holding capacity (kg/d), and is calculated as:

$$C_{WHC} = 0.230.BW - 0.000476.BW^2 \quad \text{kg DM/day} \quad (2.19)$$

taken from Whittemore *et al.* (2002). Further evidence to support WHC as an appropriate measurement for bulk can be found in Tsaras *et al.* (1998) and Whittemore *et al.* (2001a). $FI_c$ is converted from kg DM to kg feed as fed by dividing by the DM content of the feed. Actual feed intake ($FI_a$, kg/d) before any thermal constraints, (see below), is predicted as the lesser of $FI_d$ and $FI_c$, i.e., the pig will achieve its desired feed intake unless the bulkiness of the feed limits it. The effects of the thermal environment are incorporated later.

*2.3.2.2.2. Predicting growth from actual feed intake.* Where the environment is thermally neutral, the prediction of the actual rates of gain of the four body components (actual growth) can be calculated from $FI_a$ and the feed composition.

$$dP/dt = e_p.((FI_a.DCPC.v) - P_{maint}) \quad \text{kg/d}$$
$$\text{but if } dP/dt > (dP/dt)_{max}$$
$$\text{then } dP/dt = (dP/dt)_{max} \quad \text{kg/d} \quad (2.20)$$

Following the calculated protein retention, the retention of the other body components, and hence whole body growth, can be calculated.

$$dA/dt = 0.19\ dP/dt \quad \text{kg/d} \quad (2.21)$$
$$dW/dt = dP/dt.WP_m.w\ (P/P_m)^{(w-1)} \quad \text{kg/d} \quad (2.22)$$

$$dL/dt = (EI - E_{maint} - (b_p.dP/dt)) / b_l \quad kg/d \quad (2.23)$$

$$dEBW/dt = dP/dt + dL/dt + dA/dt + dW/dt \quad kg/d \quad (2.24)$$

$$dBW/dt = (dEBW/dt)/0.95 \quad kg/d \quad (2.25)$$

EI is the daily energy intake (MJ, EE/day) and equal to $FI_a$ x EEC and $b_l$ depends on whether dL/dt is positive or not. In the case of a negative value for dL/dt, the coefficient, $b_l$, is the heat of combustion of lipid that is estimated as 39.6 MJ/kg (Emmans, 1994a).

In this form there is no bound to total lipid loss. However, the fact that an animal cannot lose lipid that is not present, and must have some minimum lipid content ($L_{min}$, kg) necessary for survival, i.e. the phospholipids contained in cell walls (Napolitano and Ackman, 1992), is accounted for by assuming ($L_{min}$) to be equal to 0.1P. If the condition $L \leq L_{min}$ is reached then the rate of protein retention is reduced in order to maintain the minimum body lipid level. It should be noted that this is quite different from using the minimum lipid to protein ratio in the gain as used by some authors, including Whittemore and Fawcett (1976) and Moughan *et al.* (1987).

### 2.3.2.3. *Effect of the thermal environment*

To calculate the effect of the thermal environmental on pig performance, it is necessary to do two things. The first is to calculate the heat production (HP, MJ/d) in a non-limiting environment on *ad libitum* feeding of a feed that is described by inputs. The second is to assess the current climate in order to determine the maximum ($HL_{max}$, MJ/d) and minimum ($HL_{min}$, MJ/d) heat the pig is able lose in the given environment as defined by inputs. Comparing HP with $HL_{min}$ and $HL_{max}$ determines whether the animal is 'hot' ($HP > HL_{max}$), 'cold' ($HP < HL_{min}$) or thermoneutral ($HL_{min} < HP < HL_{max}$), and allows the appropriate action to be taken in the model. The conditions define the upper and lower boundaries of the animal's thermoneutral zone and reflect the upper and lower critical temperatures ($T_u$ and $T_l$, $^{o}C$). Pig responses to temperature included in the model are: changing posture, huddling, allowing body temperature to change within narrow limits and the regulation of evaporative heat loss from the skin and lungs. If the animal is hot then

an additional constraint on voluntary feed intake is imposed to decrease HP to that which can be lost and growth rate will be reduced below the potential of the animal. If the animal is cold an extra thermal demand, cold thermogensis, is placed upon it to meet the increased energy demands. If conditions are found to be thermoneutral no further action is taken.

*2.3.2.3.1. Calculation of heat production.* Heat production is calculated from the maintenance requirements of the pig, the heat production associated with protein and lipid retention and the direct heat increment of feeding.

$$HP = E_{maint} + (HI_P.dP/dt) + (HI_L.dL/dt) + (HI_{FI}.FI_a) \quad MJ/d \quad (2.26)$$

$HI_P$ and $HI_L$ are the heat increments of protein and lipid retention, 31.83 and 16.4 MJ/kg respectively, and $HI_{FI}$ is the heat increment of feeding calculated as the difference between MEC and EEC (MJ/kg) (Emmans, 1994a). Within the model HP is also calculated as the difference between the daily energy intake and the amount of energy retained to check the energy balance.

*2.3.2.3.2. Calculating the heat lost to the environment and assessing the current climate.* The starting point for calculating the heat exchange between pigs and their environment is the relationships developed by Bruce and Clark (1979) and Black *et al.* (1986) who extended the Bruce and Clark model for use in hot environments. Elements of the model developed by Knap (1999) have also been introduced along with further changes detailed below.

Total heat loss (HL, MJ/d) to the environment (Q) is calculated from the conductive loss through the floor ($Q_f$), evaporative heat loss from both the respiratory tract and skin ($Q_e$), radiative exchange with the building and other pigs ($Q_r$) and convective heat loss ($Q_c$). Heat loss is calculated in watts following previous thermoregulation models, but is converted to MJ/day within the model by multiplying by 11.568 to allow for a direct comparison between HP and HL.

$$Q = Q_f + Q_e + Q_r + Q_c \quad \text{MJ/day} \quad (2.27)$$

The calculation of Q is performed twice in order to calculate both $HL_{max}$ and $HL_{min}$. The numerical values used to solve the above equation are shown below. Where applicable the $_{hot}$ and $_{cold}$ subscripts are used to differentiate between those calculations used to predict $HL_{max}$ and $HL_{min}$ respectively. Where neither subscript is present the same calculation is used for both $HL_{max}$ and $HL_{min}$.

*2.3.2.3.3. Contact areas.* As the pig is able to change its posture according to environmental conditions, the contact area between each of the different surfaces has to be calculated. This follows from the pig's overall surface area (SA, $m^2$), which is calculated from BW using parameters taken from Brody *et al.* (1928) (cited by Kelley *et al.*, 1973):

$$SA = 0.097BW^{0.633} \quad m^2 \quad (2.28)$$

The proportion of surface area in contact with the floor ($A_f$, $m^2$) is dependent on the posture of the pig, with the degree of contact being related to its thermal comfort. In hot conditions the simulated animal will adopt a recumbent lying position to maximise $A_f$, and therefore maximise $Q_f$, whilst in cold conditions $A_f$ will be minimised by the animal lying on its sternum to conserve heat. Values for $A_f$ measured in hot and cold conditions by Grommers (1970) and Hsia (unpublished data in Petherick, 1983) respectively are used in the model.

$$A_{fcold} = 0.06\ SA \quad m^2 \quad (2.29)$$

$$A_{fhot} = 0.16\ SA \quad m^2 \quad (2.30)$$

Contact area with other pigs ($A_c$, $m^2$) is calculated by assuming that they huddle in the cold to maximise $A_c$ and minimise HL, whilst in the hot they avoid huddling to minimise $A_c$ and maximise HL. It is assumed that no heat is lost between pig contact areas. Although the model deals only with a single pig, other pigs present in the group are taken account of by allowing the pig to huddle if it is in a group. The

average contact area per animal in a group is dependent upon the group size, N, and, following Bruce and Clark (1979), given by:

$$A_{ccold} = 0.075\ SA((2(N-1))/N) \quad m^2 \quad (2.31)$$

$$A_{chot} = 0 \quad m^2 \quad (2.32)$$

Reliable quantification for the proportion of the skin that is wet ($A_w$, $m^2$) was unavailable in the literature, and so the estimate of Black *et al.* (1986), which assumes that the pig voluntarily wets 15 % of its skin in hot conditions, is used; $A_{whot}$ = 0.15.SA. In cold conditions it is assumed the animal will not wet its skin and a value of zero is assigned to $A_{wcold}$.

The remaining surface area of the pig is assumed to be in contact with the air ($A_a$, $m^2$) and is calculated from the total surface area of the pig minus the area in contact with the floor, other pigs and the area of wet skin. This is done for both $A_{ahot}$ and $A_{acold}$.

*2.3.2.3.4. Evaporative heat loss.* Evaporative Heat Loss ($Q_e$) is determined using equations from Bruce and Clark (1979) for the minimum evaporative heat loss ($Q_{ecold}$) and from Black *et al.* (1986) for maximum evaporative heat loss ($Q_{ehot}$). It is assumed that the ratio of HL through the lungs and skin is 50:50 for $Q_{ecold}$, whereas when the pig becomes hot it is considered to be 67:33 (Black *et al.*, 1986) due to an increase in the rate of panting.

$$Q_{ecold} = SA\ (7.4 + 0.089\ BW) \quad MJ/d \quad (2.33)$$

$$Q_{ehot} = Q_w + SA\ (12.2 + 110.8\ BW^{-0.33})X_h \quad MJ/d \quad (2.34)$$

$Q_w$ is the heat lost from wet skin (MJ/d). The variable $X_h$ relates $Q_{ehot}$ to the water content of the air, which has an adverse effect on the ability of the pig to lose heat through evaporation.

$$X_h = 1.36 - (W_{air}/35.9) \quad (2.35)$$

$W_{air}$ is the water content of the air (g/kg) calculated from standard psychometric equations (Wilhelm, 1976) using the relative humidity (RH, %) and ambient temperature ($T_a$, °C).

$$Q_w = A_w . 45.4 . \nu^{0.6} . BW^{-0.13} . (46.1 - W_{air}) \quad \text{MJ/d} \quad (2.36)$$

$\nu$ is the air speed (m/s) at animal level and the constant 46.1 g/kg denotes the air water vapour content at 39°C and 100 % relative humidity (Black *et al.*, 1986).

As $Q_e$ increases with temperature, the animal must also increase its water intake to compensate for this extra water loss. The amount of heat used to heat the extra water consumed to body temperature was calculated to determine whether or not it should be included in the model. In no case did it account for as much as one percent of the total daily HL so it was not included in the model.

*2.3.2.3.5. Heat lost to the floor and through radiation and convection.* Heat lost to the floor, ($Q_f$), through radiation, ($Q_r$), and through convection ($Q_c$) are all calculated following the equations of Bruce and Clark (1979).

$$Q_f = (A_f (T_b - T_a)) / (R_t + R_f) \quad \text{MJ/d} \quad (2.37)$$

$$Q_r = 5.3 \, A_a (T_s - T_a) \quad \text{MJ/d} \quad (2.38)$$

$$Q_c = c . A_a (T_s - T_a) \quad \text{MJ/d} \quad (2.39)$$

$T_b$, $T_a$ and $T_s$ are the deep body, ambient and skin temperature (°C) respectively, c is the convective heat transfer coefficient and calculated as, $c = 13.4 . \nu^{0.6} . BW^{-0.13}$ (Bruce and Clark, 1979), and $R_t$ and $R_f$ are the thermal resistances of the skin and different floor materials respectively, $°Cm^2/W$. Values for $R_f$ were taken from Bruce and Clark (1979) along with other values from the literature converted to terms consistent with Bruce and Clark (1979).

Bruce and Clark (1979) modelled heat exchange only in cold and thermoneutral conditions, so some of the parameters, ($T_b$ and $T_s$) had to be adapted for use in hot conditions for the calculation of $HL_{max}$ i.e. calculations of $Qf_{hot}$, $Qr_{hot}$ and $Qc_{hot}$ rather than $Qf_{cold}$, $Qr_{cold}$ and $Qc_{cold}$. Pigs are assumed to allow $T_b$ to rise from 39 °C in the cold to 40.5 °C in hot conditions (Stombaugh and Roller, 1977). The deep body thus can act as a temporary heat store. $T_s$ is estimated to be 39 °C in the hot and 32 °C in the cold (Black *et al.*, 1986).

The equations of Knap (1999) are used for tissue thermal resistance ($R_t$, °C $m^2$/W), because Knap (1999), unlike others (Bruce and Clark, 1979; Black *et al.*, 1986), relates $R_t$ directly to subcutaneous backfat depth (BF, mm) rather than to BW. The value of $R_t$ is calculated from BF, which is calculated in turn from actual body composition.

$$R_{thot} = 0.038 - (0.0001\ BF) \quad °C\ m^2/W \quad (2.40)$$

$$R_{tcold} = 0.05 + (0.002\ BF) \quad °C\ m^2/W \quad (2.41)$$

where BF is calculated from body mass and composition. Equations for BF from Knap (1999) are:

$$BF = 0.82.\ (((3.376 p_P.P) + (1.227 p_L.L)) / (0.097.BW^{0.633}))^{1.212} \quad (mm) \quad (2.42)$$

$p_P$ and $p_L$ are the proportions of body protein mass and of body lipid mass present in the subcutaneous tissue. They are calculated as $p_P = 0.1285 + 0.00286$ ln (P), and $p_L = 0.2260 + 0.1310$ ln (L) (Knap, 1999). For the purposes of the model the equations are assumed to be general across genotypes.

*2.3.2.3.6. Comparison of heat loss to the environment and heat produced.*

The calculated heat lost to the environment is compared with the HP by the pig under thermoneutral conditions to assess the pig's condition. If heat loss to the environment is greater than the heat produced through normal metabolism, i.e. $HP < HL_{min}$, then the pig is cold and the extra heat required (ExH, MJ/d) to maintain body temperature

can be calculated. When heat loss to the environment is less than that generated by normal metabolism, i.e. HP > $HL_{max}$, then the pig is heat stressed and the required reduction in heat production (RHP, MJ/d) needs to be calculated. Otherwise, when $HL_{min}$ < HP < $HL_{max}$ then the pig is thermally comfortable and no change is needed.

$$ExH = HL_{min} - HP \quad \text{MJ/d} \quad (2.43)$$

$$RHP = HP - HL_{max} \quad \text{MJ/d} \quad (2.44)$$

When the environment is found to be hot, $E_{maint}$ (Eq. 2.11) is decreased by 7.5 % to represent a decrease in physical activity of around 50 % (Knap, 1999). If the animal is found to be cold then ExH is added to $E_{Req}$ to represent the extra heat required for the pig to remain thermoneutral.

*2.3.2.3.7. Actual feed intake and growth.* Actual feed intake ($FI_a$, kg/d) can now be calculated taking into account the thermal environment. In cold conditions $FI_a$ is increased until ExH has been satisfied, or until a feed intake volume constraint is reached, in which case $FI_a = FI_c$. In hot conditions $FI_a$ is decreased iteratively until HP = $HL_{max}$. The actual growth of the pig following $FI_a$ after the evaluation of environmental constraints/demands is then calculated as before (Eqs. 2.21 to 2.25).

### *2.3.3. Running the model*

The model is set to run using the list of inputs (Table 2.1) from the start BW until the target BW is reached in daily intervals. At the end of each day the gains of each of the four components (P, L, A and W) are added to the current mass of the four body components to give the new current composition, EBW and BW. The new current composition then acts as the starting point for the next day. Any deviation between the pig's current lipid content compared to that of its desired content (Eq. 2.3) is calculated and added to $(dL/dt)_{des}$ (Eq. 2.8). This allows the pig to correct both an excess and deficit of lipid by showing compensatory thinning (Kyriazakis and Emmans 1991; Kyriazakis *et al.*, 1991b), or fattening (Stamataris *et al.*, 1991; Skiba *et al.*, 2001). The rate of rehabilitation to a desired fatness is determined only by constraints that may operate in the model. Although it is assumed that the pig will

attempt to correct instantaneously the deficit, it will usually be restricted either by the composition and bulkiness of the feed or by the hotness of the thermal environment. The main outputs from the model are given in Table 2.1.

## 2.4. Discussion

The performance of the model is compared with data from the literature in Chapter three. The discussion here will focus on the theory and concepts used in the development of the model.

The potential growth rate of the pig is described by the Gompertz growth function because of its advantages over other approaches. These are outlined in detail in Chapter one. Briefly, It allows potential growth rate to vary with the current state of the animal and not just be a constant for each genotype across a particular weight range, which was the assumption in the models of Whittemore and Fawcett (1976) and Moughan *et al.* (1987). The function needs only three parameters to describe the genotype (B and $P_m$) and current state (P) of the pig. In some models more parameters are required to describe the pig (Black *et al.*, 1986; Pomar *et al.*, 1991; Bridges *et al.*, 1992a and b; NRC 1998). Increasing the number of parameters increases the difficulty in ascribing any biological meaning to them and makes correct estimates of their values more difficult. Other things being equal, using fewer parameters is always beneficial. The Gompertz function also has the useful consequence that the weights of L, A and W in potential growth are allometrically related to P. This makes the prediction of the potential growth of the whole pig much simpler; simplicity should be seen as a key principle in any model (NRC, 1998).

The prediction of intake is important where *ad libitum* feeding is used. Of the models in the literature only those of Bridges *et al.* (1992a and b), Ferguson *et al.* (1994), Black *et al.* (1996) and Knap (1999) attempt to predict intake. Others either ignore it completely by treating intake as an input (Whittemore and Fawcett, 1976; Bruce and Clark, 1979; Moughan and Smith, 1984; Moughan *et al.*, 1987), or calculate feed intake from a singe equation (ARC, 1981; Pomar *et al.*, 1991; TMV, 1994, NRC, 1998). In these latter models, the pig's appetite needs to be characterised jointly with

the prediction for protein deposition (Pomar *et al.*, 2003). To predict intake, a model needs a sufficient description of the pig, the feed being fed and the environment it lives in. In this model the feed description includes the ideal protein content and a measure of bulkiness as well the energy content. The sufficient description of the thermal environment, which determines how much heat the pig is able to lose to the environment and consequently eat and grow, follows the approach taken by Bruce and Clark (1979) and later by Black *et al.* (1986) and Knap (1999). Aspects of the non-thermal environment, the social and disease aspects, are largely ignored; these are areas where modelling should be further pursued (Black *et al.*, 1999; Whittemore *et al.*, 2001b).

Any general growth model needs to predict the way in which scarce energy is partitioned between lipid and protein retention. In the majority of models energy is allocated independently of protein supply by assuming protein to be non-limiting (e.g. Whittemore and Fawcett, 1976; Moughan *et al.*, 1987; Pomar *et al.*, 1991; van Milgen *et al*, 2000). This of course will not always be the case and it is clearly illogical to partition energy between protein and lipid retention without taking protein supply into account. To solve this problem the rule of Kyriazakis and Emmans (1992a and b) is used, which proposes that the net material efficiency of using ideal protein is only dependent upon the ratio of MEC/DCPC of the feed. This rule was shown to be equivalent (Emmans and Kyriazakis, 1997) to the approach of de Greef (de Greef, 1992; de Greef and Verstegen, 1995), by They showed that the approach of de Greef could be predicted as a function of food protein content (at constant food energy content). The four animal parameters in the model of de Greef can be described in terms of the parameters used in the model of Emmans and Kyriazakis (1997) when predicting dP/dt and dL/dt above maintenance energy intake. Contrary to the predictions of others (Black *et al.*, 1986; de Greef, 1992; Bikker, 1994; van Milgen *et al.*, 2000) the rule of Kyriazakis and Emmans (1992a and b) predicts that all pig genotypes at all degrees of maturity follow the same rules. Experimental evidence that supports this was found (Kyriazakis *et al.*, 1994 and 1995). The rule of Kyriazakis and Emmans (1992a and b) is able to predict the widely observed occurrence of pigs gaining protein at the expense of lipid

(Stamataris *et al.*, 1991; Bikker, 1994) when energy supply is unable to fulfil both maintenance and protein retention. This is a phenomenon many partitioning rules, including those using a fixed minimum lipid to protein ratio in the gain, fail to predict (e.g., Whittemore and Fawcett; 1976, Pomar *et al.*, 1991; de Greef and Verstegen, 1995).

The model described here is one of only a few to allow for a correction to an imbalance of body composition when the pig is either fatter or thinner than desired. The model of Black *et al.* (1986) allowed compensatory gain by the inclusion of a rather unsatisfactory compensatory gain factor used to multiply potential protein deposition. The correction of an imbalance in body composition in the model is achieved by the inclusion of both compensatory lipid gain and loss. If a pig contains less lipid than is dictated by its genotype, in relation to body protein, it will attempt to correct this deficit by increasing feed intake; whereas if the pig contains an excess of lipid in its body, it will attempt to lose this by decreasing energy intake. Although in the model the pig will try and instantaneously correct any imbalance from the desired lipid to protein ratio, both compensatory lipid gain and loss will only be achieved gradually if at all. This is due to the constraints within the model, such as feed bulk capacity, maximum heat loss and the priority of protein retention over lipid.

Although there is experimental evidence that in addition to lipid, pigs are able to compensate depleted protein stores (along with the closely associated water) (Kyriazakis and Emmans, 1991; Stamataris *et al.*, 1991; Bikker *et al*, 1994), it was decided not to include this within the model. This is because of the apparent difficulties in making the necessary change of modelling pig growth around ash content (rather than protein), the only chemical component been reported not to show compensation (Kyriazakis *et al.*, 1991a; Stamataris *et al.*, 1991). If ash gain were to be used as the driver for whole body growth, then both the composition of the diet and the nutrient requirement of the pig would have to be described in terms related to ash gain (Kyriazakis and Emmans, 1992d). This proves to be difficult, as there is little information available on the nutrient and energetic requirements for ash gain

and also on the supply of the required nutrients from the diet. It is upon these grounds that the model will remain protein driven. Furthermore, using protein for the main component of growth, as is currently the case, is straightforward and allows for easy and successful calculations of pig performance. It is thought that including compensatory growth into the model to any further extent is beyond the scope of this model.

In practice, model building is an iterative process and, in this sense, model building can never be complete (Pomar *et al.*, 1991). However, it is thought that the model described here provides a good base for modelling pig performance under a wide range of thermal and nutritional environments and will readily incorporate other aspects of the environment affecting pig performance, along with any interactions between the environmental components. Further model developments will include the incorporation of the effects of the social environment including factors such as group size, stocking density, mixing and feeder space allowance. Variation between individual animals potential and in their ability to cope under differing environmental stressors will also be replicated. This will be achieved by the introduction of variation into the model, which will allow the performance of a group of individual animals to be predicted rather than simply the average pig of the particular genotype.

# Chapter 3

## Modelling the effects of the thermal environment and dietary composition on pig performance: model testing and evaluation

## 3.1. Abstract

A deterministic, dynamic pig growth model predicting the effect of genotype, the thermal and nutritional environments on the feed intake, growth and body composition of growing pigs was tested and evaluated against experimental data from the literature. Four sets of experiments meeting the necessary requirement of feeding the pigs *ad libitum* and reporting sufficient information on trial conditions were chosen to test the model. The parameters used in the model to describe the type of pig were protein weight at maturity ($P_m$), the Gompertz rate parameter (B) and the ratio of mature lipid weight ($L_m$) to $P_m$. Values for $P_m$ and B used to apply to the pigs in the four experiments were selected as those which gave the maximum daily gains equal to those reported at thermoneutral temperatures on diets not limiting in protein. The value of $L_m$ was chosen as that which gave a value for feed conversion ratio close to that seen in the experiment again at a thermoneutral temperature and on a non-limiting diet. The model was run for each of the experiments from the given start weight until slaughter weight was reached. All pigs were assumed to have their desired bodily composition at the start of the experimental period, which is determined by their genetic descriptors and weight. From the conditions of the experiments, average daily gain (ADG), average daily feed intake (ADFI), feed conversion ratio (FCR), final body weight, body composition, average daily gains of each of the chemical body components and heat production (HP) were predicted. Generally as temperature increased or the crude protein content of the feed increased, ADFI, ADG and the fatness of the pig decreased, whilst protein content increased. Quantitative differences between the model predictions and the observations were probably due to the greater sensitivity of the model to temperature. This is likely to reflect the omission of long-term adaptation and acclimatisation, or to incorrect estimation of the wetness of the pig's skin. However, model predictions were generally in good quantitative agreement with the observed data over the wide range of treatments tested. This gives support to the value and accuracy of the model for predicting pig performance when the thermal and nutritional environments are manipulated.

## 3.2. Introduction

Models of feed intake and animal growth are of interest and value to both research scientists and industry as a method of assessing and predicting performance of different kinds of animal under a wide range of conditions. By transforming concepts and knowledge into mathematical equations, and integrating them in computer programs using simulation modelling techniques, a vast store of information can be applied directly to improving the management of commercial animal enterprises and for defining research priorities (Black, 1995a). Simulation models allow the effects of a range of environmental and other variables on animal performance to be considered simultaneously in a way that cannot be done by direct experimentation. Before confidence can be placed on the predictions of a model, it needs to be tested and evaluated. Testing and evaluation of models is an extremely important and difficult exercise. The fact that a model is found to predict accurately under one set of circumstances does not mean that it is 'valid' in any general way (Black, 1995b). The more diverse the circumstances under which the model behaves well and gives accurate predictions, the more the confidence can be (provisionally) placed in it.

In Chapter two a dynamic, deterministic pig growth model designed to predict the effects of the thermal environment and feed composition on the intake and growth of pigs of different genotype fed *ad libitum* was described. The approach used builds on other growth models in the literature (Whittemore and Fawcett, 1976; Black *et al.*, 1986; Pomar *et al.*, 1991; Bridges *et al.*, 1992a and b; National Research Council, 1998; Knap 1999; Birkett and de Lange, 2001a and b), but focuses on the prediction of intake when the thermal environment and dietary composition are manipulated. The aim here is to test and evaluate this model by using several data sets from the literature. The effects of both the thermal and nutritional environments on pig performance are considered in determining the appropriateness and 'value' of the model.

## 3.3. Materials and methods

### *3.3.1. Comparison of model output with experimental data*

Methods for testing and evaluating dynamic simulation models have been discussed by Wright (1979), France and Thornley (1984), Harrison (1987) and Black (1995b). Both subjective methods, such as graphical comparisons of model predictions with experimental observations, and objective methods, such as using explicit statistical procedures, can be used. Where formal statistical procedures are used there are difficulties in choosing the most appropriate error probabilities for assessing model accuracy (Black, 1995b). Statistical procedures have been criticised (Harrison, 1987) because of their inability to prove in a statistical sense that predictions are from the same population as the experimental observations. This latter criticism arises from the difficulties in obtaining a complete description of the experimental conditions in terms used in the model. Obtaining accurate descriptions of the genotype of pig used in a particular experiment is especially difficult (Knap *et al.*, 2002).

Models cannot be validated in any general way and any apparent invalidation will always be somewhat subjective (Black, 1995b). Graphical comparisons are the main method used here to see the extent to which model predictions and experimental outcomes are in qualitative and quantitative agreement.

Experiments are of most value for the evaluation process when a large number of the inputs needed to run the model have been measured and reported (Black, 1995b). The studies used here in the evaluation process used *ad libitum* feeding, and give reasonable information on the trial conditions. The four studies used are, Nienaber *et al.* (1987a and b; further referred to as "Nienaber"), Kyriazakis *et al.* (1990; "Kyriazakis"), Ferguson and Gous (1997; "Ferguson") and Collin *et al.* (2001; "Collin"). Nienaber, Ferguson and Collin were used in the evaluation of the effects of the thermal environment. Kyriazakis and Ferguson were used to evaluate the effect of dietary crude protein content, (CPC, g/kg), on pig growth and intake. The relevant characteristics known for these studies are shown in Table 3.1, along with estimations of those not reported.

**Table 3.1.** *Characteristics of the experiments used for comparison with model predictions (values in {italics} are estimations of the values not reported)*

| | | Nienaber[a] | Kyriazakis[a] | Ferguson[a] | Collin[a] |
|---|---|---|---|---|---|
| Trial Period | BW range (kg) | 44 to 87 | 12 to 30 | 12 to 30 | 15 to 30[b] |
| Feed[c] | DE content (MJ/kg) | 13.6 | 15.8 to 17.1 | 15 | 17.6 |
| | CP content (g/kg) | 160 | 125-267 (4 levels) | 93-230 (6 levels) | 244 |
| | CP digestibility (g/g) | *{0.8}* | *{0.8}* | 0.8 | *{0.8}* |
| | Biological Value | *{0.75}* | *{0.75}* | 0.80 | *{0.75}* |
| | WHC (kg/kg) | *{3.0}* | *{3.0}* | *{3.0}* | *{3.0}* |
| | DM content (kg/kg) | *{0.88}* | 0.9 | 0.9 | 0.88 |
| Environment | Temperature (°C) | 5-30 in 5°C steps | 21.5 | 18-30 in 4°C steps | 19-35°C in 2°C steps |
| | Relative Humidity (%) | 70 (5°C) to 37 (30°C) | 40 | 62 (18°C) to 70 (30°C) | 80 (19°C) to 25 (35°C) |
| | Group Size | 2 | 1 | 1 | 3 |
| | Air velocity (m/s) | 0.12 | *{0.15}* | *{0.15}* | *{0.15}* |
| | Floor type | Wire mesh | Wire mesh | *{Concrete slats}* | Wire mesh |
| Pig[d] | $P_m$ (kg) | *{33}* | *{35}* | *{35}* | *{35}* |
| | $L_m/P_m$ (kg/kg) | *{3.0}* | *{2.5}* | *{2.0}* | *{2.5}* |
| | B ($d^{-1}$) | *{0.0100}* | *{0.0150}* | *{0.0156}* | *{0.0175}* |

[a]Nienaber *et al.* (1987a and b); Kyriazakis *et al.* (1990); Ferguson and Gous (1997) and Collin *et al.* (2001).
[b]17 days duration.
[c]DE = digestible energy; CP = crude protein; WHC = water holding capacity as a measure of feed bulk; DM = dry matter.
[d]The 3 parameters describing the pig genotype are the Gompertz rate parameter, B, protein weight at maturity, $P_m$, and the ratio of mature lipid weight, $L_m$, to $P_m$..

Nienaber worked with 60 American four-way [crossbred] females assigned at random to one of six environmental temperatures (5 to 30 °C) at 44 kg. The pigs were slaughtered at 87 kg body weight (BW, kg). Final chemical composition, average daily gain (ADG, kg/d), average daily feed intake (ADFI, kg/d), average feed conversion ratio (FCR, kg feed /kg gain) and average daily water use (ADWU, kg/d) were all recorded. Heat production (HP, MJ/d) was also measured by indirect calorimetry on each pen three times during the study.

Kyriazakis used 40 Cotswold F1 hybrid [Large White x Landrace] pigs consisting of entire males and females on four dietary treatments where dietary protein level ranged from inadequate to excessive. All pigs were kept at the same temperature and slaughtered at 30 kg. Measurements recorded were final BW, ADFI, ADG and FCR.

Ferguson used 99 entire male pigs [Large White x Landrace] in a 4 x 6 factorial experiment. The respective factors were four temperatures, 18, 22, 26 and 30 °C, and six dietary CPC's ranging from 0.48 to 1.2 times the estimated amino acid requirements of the pigs. All animals were kept until a slaughter weight of 30 kg liveweight. Final BW and chemical composition, ADG, ADFI, FCR and rates of gain of the four chemical components were reported. As Ferguson reported little or no significant interaction between the dietary and thermal treatments in this experiment (Tables 4 to 6 in Ferguson and Gous, 1997) the results were pooled across both factors in turn to allow both to be investigated independently.

Collin used 105 crossbred [Pietrain x (Large White x Landrace)] castrates and females to determine the effects of a 17-day exposure to one of nine environmental temperatures (19 to 35 °C). Final BW, ADFI, ADG, FCR and ADWU were all recorded.

The parameters used in the model to describe the kind of pig are protein weight at maturity ($P_m$, kg), the Gompertz rate parameter (B, $d^{-1}$) and the ratio of lipid to protein weight at maturity ($L_m/P_m$, kg/kg). The meaning of these parameters is described in detail in Chapters one and two. None of the experiments used gives descriptions of the genotypes used in these terms, which is a common problem (Knap, 1999, Knap *et al.,* 2002). Values for the pig parameters had necessarily to be estimated from inadequate data. The values of $P_m$ and B used to apply to the pigs in the 4 experiments were calculated to be those which gave maximum daily gains equal to those reported at thermoneutral temperatures on diets not limiting in protein. The value of $L_m$ was chosen as that which gave an FCR value in close agreement to that seen in the experiment at a thermoneutral temperature and on a non-limiting diet.

For the other parameter values not reported, values representative of a typical pig diet and environment were assumed. A value of three was assumed for the water holding capacity (WHC, kg/kg), (Whittemore *et al.,* 2002), 0.75 for biological value (v) (Boisen *et al.,* 2000), 0.80 for crude protein digestibility ($CP_d$, kg/kg), (Ferguson and Gous, 1997), 0.88 for dry matter content (DM, kg/kg), (Collin *et al.,* 2001) and 0.15 for air velocity (v, m/sec), (Knap, 1999).

The model was run for each of the four experiments from the given start weight until slaughter weight, or time in the experiment of Collin, was reached. Body composition at the start of the experimental period was assumed to be that calculated from their initial weight and the estimated genetic descriptors. From the conditions (actual and assumed) of the experiments, ADG, ADFI, FCR, final BW and body composition, average daily gains of each of the chemical body components and HP were predicted.

## 3.4. Results

### *3.4.1 Effect of the thermal environment*

*3.4.1.1. Voluntary feed intake, daily gain and feed conversion ratio.* Figures 3.1a to 3.1c show the observed and predicted effects of temperature on ADFI and ADG for Ferguson, Nienaber and Collin respectively. The simulated ADFI and ADG values for all data sets follow the direction of change observed. Above the estimated upper critical temperature, the values of both variables decrease with increasing environmental temperature. Within the estimated thermoneutral zone little change is seen. Predictions of the absolute values for ADFI and ADG were in better agreement with the observed data within the estimated boundaries of the thermoneutral zone, than outside. The experimental ADFI's and ADG's of Nienaber and Ferguson were lower than was predicted by the model, while the reverse was the case with the Collin experiment. Actual rates of change in ADFI and ADG with increasing temperature were generally in close agreement with the values observed, especially for the prediction of intake. The observed (and predicted) decreases in feed intake (g/deg C d) were (i) Nienaber, 5 to 30 °C, 41 (38) (ii) Ferguson, 18 to 30 °C, 24 (25) and, (iii) Collin, 19 to 35°C, 40 (38). Over the same temperature ranges, the observed

(and predicted) decreases in gain were (g/deg C d) (i) Nienaber, 10 (2) (ii) Ferguson, 7 (14) and, (iii) Collin, 28 (28).

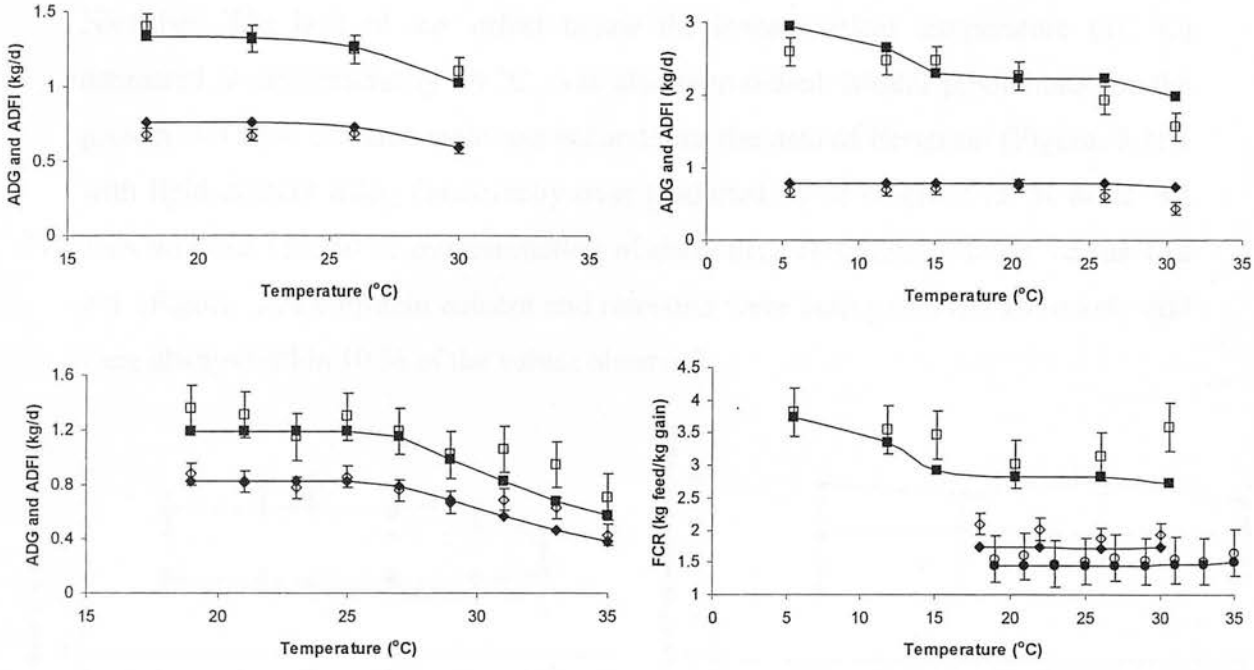


**Figure 3.1.** *Observed (± sd) (□,◇) and predicted (■, ♦) effects of temperature on the average daily feed intake (ADFI) (□,■) and average daily gain (ADG) (◇,♦) for; (A) Ferguson and Gous (1997); (B) Nienaber et al. (1987); (C) Collin et al., (2001), and; (D) Observed (◇, □, ○) and predicted (♦,■,●) effects of temperature on the feed conversion ratio (FCR) for the pigs of Nienaber et al. (1987) (□,■), Ferguson and Gous (1997) (◇,♦) and Collin et al. (2001) (○,●).*

The FCR's predicted by the model were in reasonable agreement with the observed FCR's for all three data sets (Figure. 3.1d), and were closest for the data of Collin. The model generally underestimated FCR for the data of Ferguson underestimated the increased FCR seen at the highest temperature for the data of Nienaber.

*3.4.1.2. Protein and lipid contents.* As no data on body composition were collected by Collin, the model's predictions could be compared only with the data sets of Nienaber and Ferguson. Agreement, both qualitatively and quantitatively, with the observed data of Nienaber on final body composition (Figure. 3.2a) was very close, with predicted observations always being well within 10 % of that

observed. The model reproduced the observed decrease in percentage lipid, and increase in percentage protein, as the temperature increased above the estimated upper critical temperature ($T_u$, °C) estimated as approximately 28 °C for the pigs of Nienaber. The lack of any effect below the lower critical temperature ($T_l$, °C) estimated at approximately 16 °C, was also reproduced. Model predictions for the protein and lipid contents were less accurate for the data of Ferguson (Figure. 3.2b), with lipid content being consistently over predicted by as much as 20 % at 22 °C. This was due to a 50 % overestimation of daily lipid retention, 190 g/d versus 122 g/d. (Figure. 3.2c). Protein content and retention were both predicted accurately and were always within 10 % of the values observed.

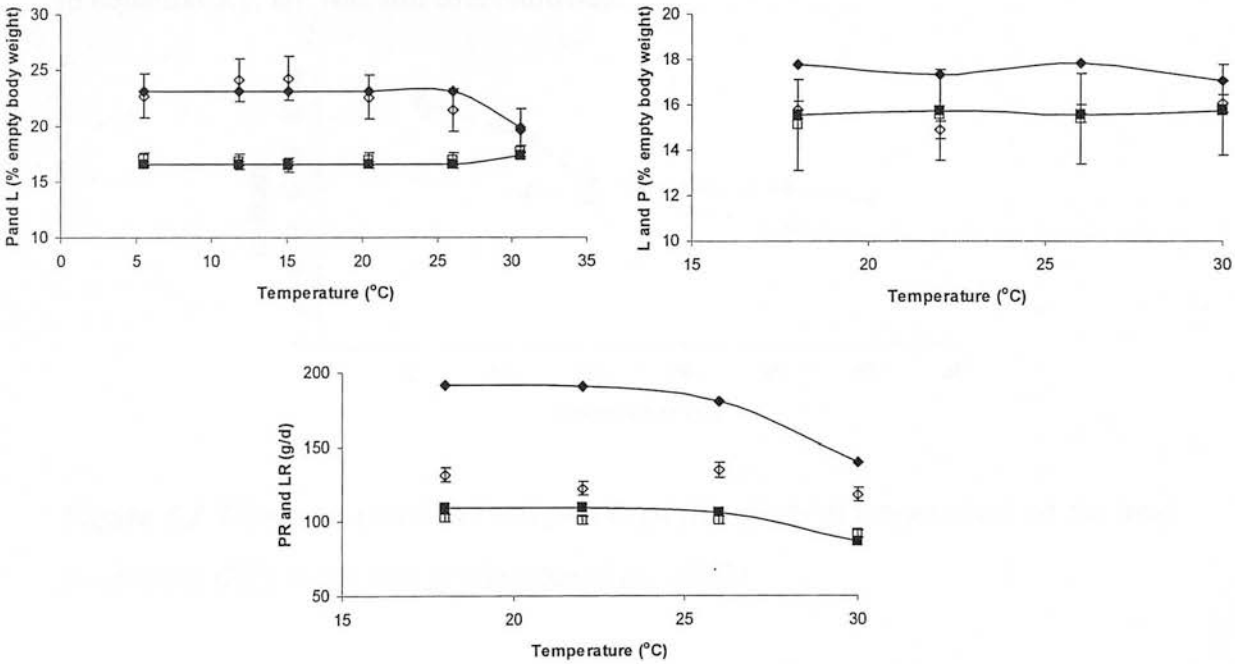


**Figure 3.2.** *Observed (± sd) (□,◇) and predicted (■, ♦) effects of temperature on final body protein (P) (□,■) and lipid content (L) (◇,♦) for the pigs of; (A) Nienaber et al. (1987), and; (B) Ferguson and Gous (1997). (C) Observed (□,◇) and predicted (■, ♦) rates of gain of protein (PR) (□,■) and lipid (LR) (◇,♦) retention for Ferguson and Gous (1997).*

*3.4.1.3. Heat production.* Nienaber derived a multiple linear equation based upon their data collected by indirect calorimetry to predict the HP of their pigs under the differing experimental temperatures. The regression equation using three

independent variables ($BW^{0.75}$, voluntary feed intake, VFI, kg/week and temperature of the environment, $T_a$, °C) was estimated as:

$$HP = 10.80 + 0.337BW^{0.75} - 0.272T_a + 0.150VFI \quad MJ/d \quad R^2 = 0.82, \qquad (3.1)$$

The model predicts values for treatment means that are in good qualitative agreement with those calculated using equation 3.1. Heat production is predicted to decrease with increasing temperature (Figure. 3.3), but the absolute values from equation 3.1 are lower than those predicted by the model. Over prediction of HP was not due to the over prediction of ADFI, as when model predictions for ADFI were used for VFI in equation 3.1, HP was still overestimated.

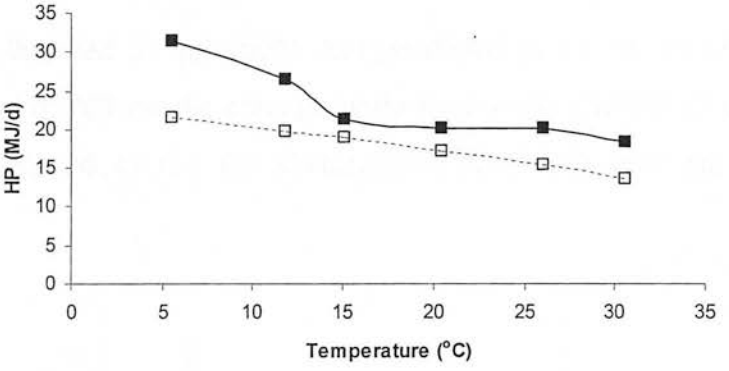


***Figure 3.3**. Observed (± sd) (■) and predicted (□) effects of temperature on the heat production (HP) of the pigs of Nienaber et al. (1987).*

### *3.4.2. Effect of dietary crude protein content*

*3.4.2.1. Voluntary feed intake, daily gain and feed conversion ratio.* The model predicts a decrease in ADFI as the protein content of the diet increases and this is in good qualitative agreement with both sets of observed data (Figures. 3.4a and b). Quantitatively the agreement is closer to the observations of Ferguson than to those of Kyriazakis, but ADFI is over predicted for both experiments on low protein feeds. ADFI was over predicted by 25 and 30 % on the lowest protein diets for the experiments of Ferguson and Kyriazakis respectively. Predicted ADG is in better agreement with the observations of Ferguson (Figure. 3.4b) than for the observations of Kyriazakis (Figure. 3.4a), but both are again over predicted on the lower protein

feeds. The model predicts a relatively constant ADG with varying CPC whereas experimental observations showed an increase in ADG as CPC increased. The FCR values predicted by the model are in reasonable quantitative agreement with the observed for both experimental data sets. Both predicted and actual FCR decreased as the CPC of the diet increased (Figure. 3.5).

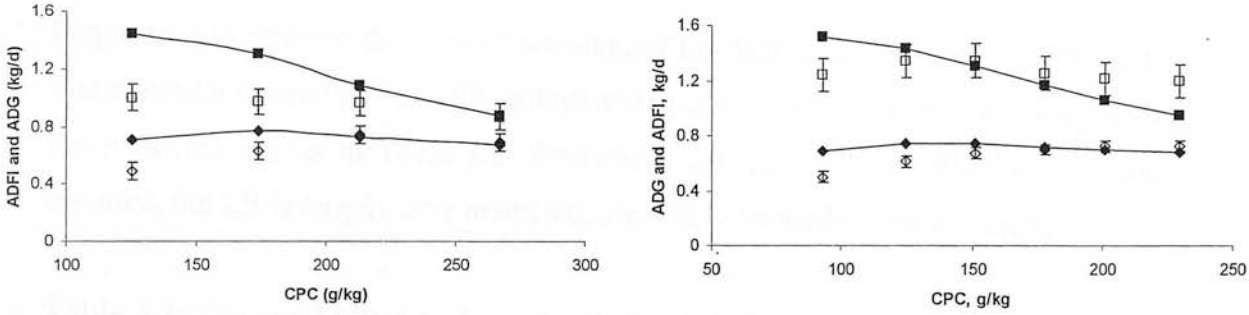


**Figure 3.4.** *Observed (± sd) (□,◇) and predicted (■,◆) effects of dietary crude protein content (CPC) on the average daily feed intake (ADFI) (□,■) and average daily gain (ADG) (◇,◆) for; (A) Kyriazakis et al. (1990), and; (B) Ferguson and Gous (1997).*

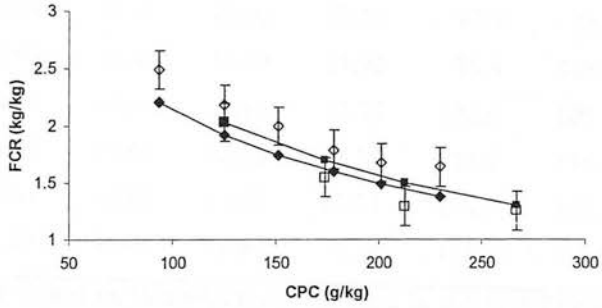


**Figure 3.5.** *Observed (± sd) (□,◇) and predicted (■, ◆) effects of dietary crude protein content (CPC) on the feed conversion ratio (FCR) for the pigs of Kyriazakis et al. (1990), (□,■) and Ferguson and Gous (1997) (◇,◆).*

*3.4.2.2. Protein and lipid content.* The predicted and observed chemical composition of the empty body of Fergusons pigs at 30 kg live weight is shown in Table 3.2. Both predicted and observed results show that as the dietary protein concentration of the diet increases, there is an increase in the protein content of the body and a corresponding decrease in lipid content. It can be seen clearly that the

predicted results are in better agreement with the observed data for protein content than that of lipid, with lipid content generally being over predicted. Empty body lipid content was over predicted by approximately 20 % (observed value of 23 % versus predicted value of 28 %) on the lowest protein diet, 93 gCP/kg. Predictions for water and ash content were in good agreement with the observed data (not shown).

Ferguson also reported the rates of retention of the four chemical body components. The retention rates of protein (PR, g/day) and lipid (LR, g/day) are shown along with the predicted values in Table 3.2. Predictions for both LR and PR follow those reported, but LR is largely over predicted, especially on the low protein diets.

**Table 3.2**: *Observed (Obs) and predicted (Pred) body composition (% empty body weight), protein retention (PR, g/d) and lipid retention (LR, g/d) of pigs from Ferguson and Gous (1997) fed on feeds differing in crude protein content (CPC, g/kg)*

| CPC (g/kg) | Protein (% EBW) | | Lipid (% EBW) | | PR (g/d) | | LR (g/d) | |
|---|---|---|---|---|---|---|---|---|
| | Obs[a] | Pred | Obs[a] | Pred | Obs[a] | Pred | Obs[a] | Pred |
| 93 | 13.53 | 13.40 | 23.00 | 28.12 | 57.9 | 75.2 | 163.6 | 287.1 |
| 125 | 14.99 | 14.67 | 18.70 | 21.92 | 85.8 | 945.2 | 151.6 | 237.4 |
| 151 | 15.70 | 15.60 | 15.85 | 17.76 | 102.6 | 105.3 | 139.6 | 191.3 |
| 178 | 16.37 | 15.80 | 13.33 | 16.33 | 111.9 | 110.3 | 113.0 | 145.6 |
| 201 | 16.43 | 16.80 | 12.03 | 11.91 | 116.7 | 113.5 | 103.6 | 112.9 |
| 230 | 16.51 | 17.45 | 10.64 | 9.14 | 117.8 | 116.8 | 88.2 | 79.6 |

[a]standard deviations of % protein, % lipid, PR and LR are 2 %, 0.4 %, 1.72 g and 4.11g respectively

## 3.5. Discussion

The aim of this Chapter was to evaluate the deterministic and dynamic model of pig growth described in Chapter two. The predictions of the model were compared with the outcomes of experiments. It is thought this method of evaluation is more useful than a conventional 'sensitivity analysis'. Data sets from the literature were used to assess the suitability of the model for predicting the voluntary feed intake and performance of growing pigs in differing environmental conditions and on foods of differing composition. The data sets were chosen on the basis that they used *ad libitum* feeding and described trial conditions in reasonable detail.

### 3.5.1. The thermal environment

The model correctly predicted the direction of response of growth and intake in the experiments and this should be regarded as giving some support to the model's adequacy. Generally, the model predicts that, as temperature increases beyond $T_u$, ADFI, ADG and HP all decrease. Within the zone of thermal comfort, no effects of temperature are predicted. These trends suggested by the model were seen in all of the experimental data sets.

In hot environments, when $T_a > T_u$, the thermoneutral HP cannot all be lost to the environment and HP must be reduced to avoid a hyperthermic rise in body temperature (Knap, 1999). Consequently, reduced rates of protein and lipid deposition, and a reduction in ADFI, are predicted with increasing environmental temperature. The decrease in ADFI above $T_u$ can be dramatic. Collin reported an average decrease in ADFI of 59 g/ deg C d between 25 and 35 °C for pigs weighing 16 to 30 kg. When the model was used to simulate these two temperatures of Collin a reduction of 61g/ deg C d was predicted in good agreement with that observed. Sugahara *et al.* (1970) reported a decrease of 42 g/ deg C d between 22 and 33 °C for pigs weighing 9 to 34 kg. These values are also consistent with those predicted by the model and seen in the experiments of Nienaber and Ferguson.

In cold environments when $T_a < T_l$, thermoneutral HP is not sufficient to meet the environmental heat demand and extra heat must be produced for cold thermogenesis. This is achieved by an increase in feed intake. Providing that ADFI can be increased sufficiently to meet the extra costs of cold thermogenesis, i.e. no feed bulk constraint is met, then ADG will remain constant below $T_l$. No decreases in ADG were predicted or observed, as temperatures in the experiments were not low enough for any intake constraints to be reached on the low bulk feeds used. For example, in the experiment of Nienaber no significant decrease in ADG was observed as the temperature was decreased below $T_l$ ($\approx$16 °C) although a significant increase in ADFI was observed.

Although model predictions for ADFI and ADG generally agreed with the experimental results, there were important cases of lack of fit. The most likely cause of inaccurate predictions for the data of Nienaber and Collin outside the zone of thermoneutrality is the inaccurate estimations of the minimum ($HL_{min}$, MJ/d) and maximum heat losses ($HL_{max}$, MJ/d) of the pig in the particular environment. It has been noted that in hot conditions pigs will try and wet their skin with either drinking water or urine in an attempt to cool themselves (Mount *et al.*, 1971; Giles *et al.*, 1988; Nienaber *et al.*, 1996). This phenomenon is currently included in the model, with an upper limit of 15 % of the pig's surface area being able to be wet ($A_w$, $m^2$) under hot conditions, following Black *et al.* (1986). However, as the value of this important parameter appears never to have been measured (Knap, 1999), the estimate used cannot lay any claim to being accurate. The differences between the simulated and experimental results of Nienaber and Collin are in different directions. This could be accounted for if the value assigned to $A_w$ was overestimated for the pigs of Nienaber and underestimated for the pigs of Collin. Evidence from the experiment of Collin suggests that the pigs did indeed wet themselves to a greater extent at the higher temperature as measured water use increased from 2.62 kg/d at 19 °C to as high as 6.06 kg/day at 33°C.

To quantify the effects of increasing heat loss (HL, MJ/d) from wet skin in the model, the value of $A_w$ was increased incrementally from 15 % to an upper limit of 50%. The value of this parameter thus became an input into the model. The results generated for ADG (Figure 3.6) show that increasing $A_w$ up to 25 % allowed the predictions to match very closely those observed by Collin. The same result was seen for the prediction of ADFI (not shown). Although this may or may not be evidence that the model estimate of $A_w$ is responsible for inaccuracies in prediction, what it does highlight is the sensitivity of the model to $A_w$ and the importance in choosing correct parameter estimates.

Whether a particular parameter within the model is assigned a fixed value, or whether it is made a variable to be input, is an important point that illustrates one of the problems of modelling. It is preferable to incorporate the effects of an observed

phenomenon, such as wetting, in the model as a central estimate from the currently available information, rather than to tailor the values of model parameters to those that make the model fit a particular experiment. This is because it is by better understanding a model, and highlighting its failings, that we can identify areas where further research is needed and progress in animal modelling can be made.

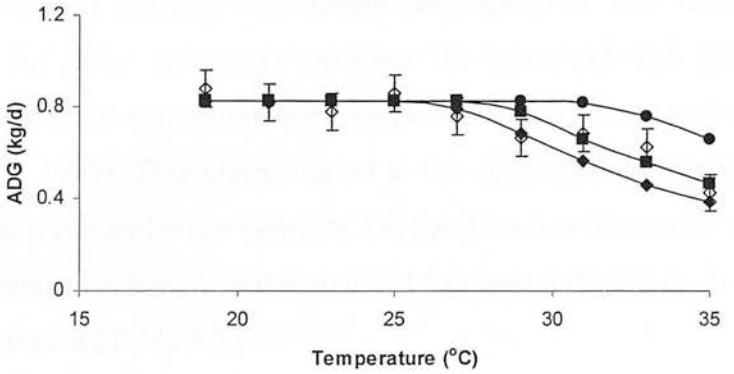


**Figure 3.6.** *The effect of increasing the percentage wet skin ($A_w$) on the average daily gains (ADG) (◇) of the pigs of Collin et al. (2001). The symbols (◆,■,●) represent predicted the ADG at 15, 25 and 50% $A_w$ respectively.*

The model shows good qualitative agreement with the data of Nienaber for the effects of the thermal environment on body composition. The actual changes in the percentages of protein and lipid in the empty body as temperature increased were well predicted by the model. The decrease in ADFI predicted to occur with increasing temperature will necessarily result in less lipid being retained as there is less energy available for lipid retention after both maintenance and protein retention have been accounted for. The model is able to predict this change in body composition with temperature due to the use of the chosen partitioning rule, which allows pigs to forego lipid gain to support protein gain (Kyriazakis and Emmans, 1992). Quantitatively the predictions of the protein and lipid contents of the body were very close to those observed. This also suggests that the value chosen for the mature lipid to protein ratio of the pig, $L_m/P_m$, was likely to have been accurate.

Model predictions for the protein content at the end of the trial period agree closely with the data of Ferguson, whereas predictions for lipid content are poor. Empty body lipid content was largely over predicted, particularly at the higher temperatures. It is thought that this is not a result of an inaccurate estimation of $L_m/P_m$. There is no obvious explanation for the discrepancy in this particular case. Values predicted for ash and water content matched very closely those observed. This is to be expected to follow from the close agreement between the observed and predicted protein contents, and the close association between protein and both ash and water (Emmans and Kyriazakis, 1995). This gives support to the calculations used in the model for the calculation of ash and water contents. On the diets low in protein, the rate of lipid retention was considerably overestimated and this was reflected in an overestimation of final lipid content (Table 3.2.).

### *3.5.2. Nutritional environment*

The model predicts that intake will increase with a reduction in feed ideal digestible crude protein content as the pig attempts to continue to satisfy its protein requirements for potential growth and maintenance. The constraint of feed bulk was not reached in the model simulations of the real experiments, while heat loss constraints were reached only at the highest temperature in the experiment of Ferguson. The predictions of the model matched more closely the experimental observations of Ferguson, while substantially overestimating ADFI, and consequently ADG, for the experimental data of Kyriazakis. The FCR's were predicted well in both cases, being almost linearly related to CPC.

The increase in ADFI on foods low in protein reported by Kyriazakis and seen in other experiments (Kyriazakis *et al.*, 1991; Schenck *et al.*, 1992a and b), was smaller than the change predicted by the model. It must be assumed that the size of some constraint acting on intake is underestimated in the model. The only constraints in the model are bulk and heat. It was possible to make the model replicate the observed ADFI's and ADG's of Kyriazakis by increasing the bulk content of the feeds used. However, Kyriazakis reported (personal communication) that it was unlikely that the bulkiness of the feeds used was in fact a limitation to ADFI. This means that the

discrepancy can be accounted for only as being due to a constraint on heat loss acting differently in the model than in the actual experiment. It is possible that the assumptions made in the model about evaporative heat loss did not apply in the experiment. Any such difference could account for differences between observed and predicted performance. The model was re-run with the amounts of both panting that the pig performed and $A_w$ being decreased. These alterations shifted the response in the expected direction, but still failed to decrease ADFI and ADG to the levels observed on low protein feeds in the experiment.

The model assumes that adaptation and acclimatisation will both occur immediately, and can be maintained indefinitely. For functions such as keeping the body wet and maintaining high rates of panting, this may be too simplistic. Therefore, the predicted $T_u$, which is calculated from maximal heat loss, is not necessarily representative of a true $T_u$ able to be tolerated for lengthy periods. Because adaptation and acclimatisation both occur over time, over a period of unknown duration, and to differing degrees depending upon circumstances, they are difficult to include in model simulation. However, as Whittemore *et al.* (2003) point out in their attempt to model feed intake and performance during the period of adaptation to a new food, 'the adaptation period has important implications for the intake and performance of pigs'. This is an area of research that has seen little development and an area where modelling could productively be pursued.

The model's predictions of the protein and lipid contents of the empty body matched qualitatively those observed in the experiment of Ferguson, with protein content decreasing and lipid content increasing as CPC decreased. Pigs given a diet sub-optimal in CPC were also found to be fatter and contain less protein at a given weight by Campbell (1977), Campbell and Dunkin (1983), and Kyriazakis and Emmans (1991 and 1992). However, whilst PR and body protein content are predicted accurately by the model, LR and body lipid content are over predicted. The model predicted higher values for ADFI than were observed on the low protein diets, and consequently daily energy intakes were higher which enabled the deposition of excess lipid. The discrepancy between the observed and predicted ADFI on low

protein diets is unclear, as it would be expected that the pigs would maximise their intakes, enabling them to maximise protein intake and consequent growth.

Generally the predictions of the model are in good agreement with observed data and show correct qualitative agreement. This indicates that the model logic is working correctly. Quantitative agreement is often, but not always, close and there are occasions where the model fails to predict accurately results seen in the literature. Possible reasons include the considerable uncertainty in the initial estimation of $A_w$, and the difficulty involved in predicting how its value may change with adaptation. In addition the value of $A_w$ may vary between treatments and experiments. The model is thought to be an advance over others due to the incorporation of a good partitioning rule and compensatory lipid growth, and adequate descriptions of the both the thermal and nutritional environments whilst maintaining simplicity and flexibility. Lastly, the model is able to predict the voluntary feed intake of pigs, which is a necessity if we are to understand the practical value of changes in either management conditions or the pig as it grows (Kyriazakis, 2003).

# Chapter 4

## Predicting the consequences of social stressors on pig food intake and performance

## 4.1. Abstract

The influence of social stressors on pig performance, although undeniable, is frequently underestimated, and in pig growth modelling is generally ignored. The aims here were to quantify the effects of the main social stressors, i.e., group size, space allowance, feeder space allowance, and mixing on the performance of growing pigs and to incorporate these relationships into a general growth simulation model. Effects of the individual stressors were described by conceptual equations derived on biological grounds. Parameter values were estimated from experimental data while taking steps to avoid the problems of using a strictly empirical approach. It was assumed that social stress decreases the capacity of the animal to attain its potential. This is equivalent to lowering the maximum rate of daily gain ($ADG_p$). As it is generally assumed that animals eat to attain their potential, a decrease in $ADG_p$ necessarily leads to a decrease in intake. Genetic variation between genotypes in their ability to cope with social stressors was accounted for by introducing an extra genetic parameter (EX) in the model. The value of EX adjusts both the intensity of stressor at which the animal becomes effectively stressed, and the extent to which stress reduces performance and increases energy expenditure at a given stressor intensity. Rather than using an empirical adjustment to predict values for the model output variables, such as intake and gain, the chosen functional forms were integrated into a general growth model as mechanistic equations. This allowed the effects of interactions that exist between social stressors and the other variables, such as the genotype, feed composition and environment on pig intake and growth, to be explored and, at least in principle, predicted. The adapted model is able to predict the performance of pigs differing in both potential and ability to cope with environmental stressors when raised under given dietary, physical and social environmental conditions. The social stressor equations developed here may be incorporated into other pig growth simulation models.

## 4.2. Introduction

The performance of commercial pigs is often below that seen under good experimental conditions. Campbell and Taverner (1985) found growth rate to be 28% lower in commercial units than in experimental conditions. At least some of this

decrease in performance can be attributed to environmental stressors. The word 'stressor' is used with no implication about any specific physiological mechanism. Quantifying stressor effects may allow the removal of constraints that prevent pigs achieving their potential and substantially increase the profitability of pig enterprises.

Stressors in the physical environment have been comprehensively modelled (e.g., Black *et al.*, 1986) allowing predictions of performance under varying conditions to be made. However, social stressors, including group size (N), space allowance (SPA, $m^2/BW^{0.67}$), feeder space allowance (FSA, feeders/pig), and mixing, have been largely ignored, mainly due to a lack of quantitative data on which to build models and a lack of understanding of how such stressors affect performance. The effects of N and SPA have been considered for their effects on heat exchange (e.g., Black *et al.*, 1986) and the model of NRC (1998) includes a social stressor effect on performance, with SPA directly affecting dietary energy intake. However, this is considered to be ' a crude estimate [which] should be used with caution' (NRC, 1998). Kornegay and Notter (1984) developed regressions relating performance to SPA and N for pigs in three weight ranges, but these equations are difficult to interpret and implement (Chapple, 1993), and they fail to predict interactions between the type of pig and the environment in which it is kept.

The aims of this Chapter were to quantify the effects of social stressors on the performance of growing pigs, including variation in their ability to cope, and to incorporate these relationships into a more general growth model described in Chapter two to allow the prediction of more complex interactions.

## 4.3. Materials and Methods

### *4.3.1. Representing the effects of social stressors on performance*

It is assumed that social stress decreases the animal's capacity to attain its potential, an 'upper-limit' defined by the animal's genotype. This is equivalent to lowering the maximum rate of daily gain ($ADG_p$, kg/d) that the pig is able to achieve. The food intake needed for $ADG_p$ is the desired feed intake ($FI_d$, kg/d) (Kyriazakis and Emmans, 1999). A decrease in $ADG_p$ is assumed to necessarily lead to a decrease in

$FI_d$. In the model food intake is directly affected only when FSA is limiting and constrains intake.

### *4.3.2. Choice of functional form and parameter estimation*

Rather than predicting values for the model output variables, such as daily intake and gain by an empirical adjustment, a different approach used here integrates the chosen functional forms into a general growth model as mechanistic equations. This method allows any interactions that exist between the type of pig (i.e., its potential) and its environment to be explored and, at least in principle, predicted.

Experimental data were used to test the chosen functional forms for their relevance, and to enable realistic quantitative values to be assigned to the parameters (Table 4.1). To avoid the various problems of using a strictly empirical approach, several measures were taken:

(i) by only using either experiments where all variables other than the one of interest were controlled for or experiments designed using a factorial method, in the analysis. This method was chosen to avoid the confounding effect of variables, especially N and SPA;

(ii) by using more biologically sound methods where possible. For example, the method proposed by Petherick (1983) was used for calculating the effect of SPA on performance. This method relates SPA to the spatial requirements of pigs according to body weight (BW, kg) rather than simply area per pig;

(iii) by taking differences in BW into account. Relative daily gain (R, $d^{-1}$) is used as the measure of performance rather than daily gain, thus eliminating the need for separate equations according to BW. This also allows a greater amount of information to be used in the analysis;

(iv) by calculating R relative to the performance seen at the lowest degree of stressor in each experiment. This accounts for differences in the potential of pigs used in the different experiments;

(v) by using a statistical model within GenStat (GenStat $5^{th}$ edition, 2001), to account for differences between the experiments and to give appropriate weighting for the number of replications in each experiment. A necessary

assumption of using a naive empirical approach is that all experiments summarised were carried out under the same conditions, (i.e., they are all replicates of the same experiment);

(vi) by checking that the equations used are sensible when extrapolated over the full range of interest.

**Table 4.1.** *Parameter values for the conceptual equations relating the major social stressors to pig performance estimated from experimental data in the literature*

| Equation[a] | | Parameter 1 | Parameter 2 | Parameter 3 | $R^2$ |
|---|---|---|---|---|---|
| 4.2 | $R_{SPA} = b_1 + g_1 \ln (SPA)$ | $b_1 = 168.49$ (9.62)[b] | $g_1 = 21.48$ (2.65)[b] | - | 87.9 |
| 4.3 | $R_N = b_2 - g_2 \ln (N)$ | $b_2 = 100$[c] | $g_2 = 3.6971$ (0.69)[b] | - | 54.6 |
| 4.4 | $E_N = (x_1.(N-1)).E_{Maint}$ | $x_1 = 0.0075$ | - | - | NA |
| 4.8 | $FR_{max} = (g_3.BW^1) / (WHC \times 1000)$ | $g_3 = 2.85$ | - | - | NA |
| 4.1 1 | $R_{Mix} = b_3 - g_4.BW - ((g_5.BW).\ln.(t))$ | $b_3 = 100$[c] | $g_4 = 0.6$ | $g_5 = 0.18$ | NA |
| 4.1 2 | $E_{Mix} = (x_2 - (x_3.\ln.(t))).E_{Maint}$ | $x_2 = 1.15$ | $x_3 = 0.050$ | - | NA |

[a] $R_{SPA}$, $R_N$ and $R_{Mix}$ represent the relative daily gain as a percentage of maximal performance in relation to space allowance (SPA, $m^2/BW^{0.67}$), group size (N) and mixing (Mix) respectively. $E_{Maint}$, $E_N$ and $E_{Mix}$ represent the energy expenditure (MJ/d) due to maintenance, group size and mixing respectively. $FR_{max}$ is the maximal feeding rate (kg/min) and WHC is the water holding capacity (kg/kg) of the food used as a measure of its bulk.

[b] Values in brackets are standard errors.

[c] Denotes fixed parameter values.

### *4.3.3. Space Allowance*

The approach devised by Petherick (1983) was used to achieve a biological description of space requirements rather than simply using area per pig. It is based on the spatial requirement of pigs, dependent upon their BW, and has physiological significance since pigs use postural changes to broaden their zone of thermal comfort. The effective space allowance per pig is calculated as:

$$SPA = Area / BW^q \quad (4.1)$$

where Area is $m^2$/pig and q is the body weight scalar calculated to be 0.67 (Petherick, 1983).

Decreasing SPA depresses intake and growth (Edwards *et al.*, 1988; Gonyou and Stricklin, 1998). The extent may depend on the type of pig. It is assumed that there is a critical value for SPA, ($SPA_{crit}$, $m^2/BW^{0.67}$) below which performance becomes depressed. Solid floors have a greater $SPA_{crit}$ than partially or totally slatted floors (Turner *et al.*, 2000) mainly due to pigs avoiding lying in dung (Spoolder *et al.*, 2000). It is assumed that above $SPA_{crit}$, SPA has no effect on performance. Growth rate goes to zero when SPA reaches $SPA_{min}$ ($m^2/BW^{0.67}$). The value assigned to $SPA_{min}$ is the area required for pigs to lie on their sternum, 0.019 $m^2/BW^{0.67}$ (Petherick, 1983). When $SPA_{min} < SPA < SPA_{crit}$, relative daily gain ($R_{SPA}$, $d^{-1}$) in relation to that recorded at a $SPA > SPA_{crit}$, is calculated as:

$$R_{SPA} = b_1 + g_1 f(SPA) \quad (4.2)$$

The values of $b_1$ and $g_1$ are affected by genotype. The shape of the relationship between $SPA_{crit}$ and $SPA_{min}$ was chosen after inspection of experimental data.

All experiments used in the analysis varied pen area with a fixed group size and were carried out on floors that were either partially or fully slatted. The few studies that used solid floors were omitted (Table 4.2). The value assigned to $SPA_{crit}$ was 0.039 $m^2/BW^{0.67}$. This is the value proposed by Gelbach *et al.* (1966) and is consistent with the values proposed by Edwards *et al.* (1988) and Gonyou and Stricklin (1998) of 0.034 and 0.039 respectively. It is also within the range proposed by Black *et al.* (1995) of 0.035 to 0.039 $m^2/BW^{0.67}$. A log regression equation gave the best fit and was chosen for the prediction of performance below $SPA_{crit}$ (see Table 4.1). To take account of the greater space requirements of pigs housed on solid floors, SPA in equation 4.2 is decreased by 25 % in agreement with Whittemore (1998) when pigs are housed on solid floors.

**Table 4.2.** *Data used to develop and evaluate the effect of space allowance on pig performance*

| Source | Average BW and BW range, kg | Group size | Space allowance, $m^2/BW^{0.67}$ [a] |
|---|---|---|---|
| NCR-89, (1993)[b] | 83.5 (54 to 113) | 10, 10, 8 | 0.029, 0.038, 0.048 (Set) |
| Edmonds *et al.*, (1998) | 72.5 (18 to 127) | 8 | 0.022, 0.036 (Stepped) |
| Edwards *et al.*, (1998) | 59.5 (34 to 85) | 12 | 0.024, 0.027, 0.03, 0.034 (Stepped) |
| Gonyou and Stricklin (1998) | 61.0 (25 to 97) | 3, 5, 6, 7, 10, 15 | 0.030, 0.039, 0.048 (Stepped) |
| Hyun *et al.*, (1998) | 45.5 (36 to 55) | 8 | 0.019, 0.043 (Set) |

[a]Set and stepped space allowance refers to experiments where pen area remained fixed throughout and where pen area was increased to maintain a constant space per $BW^{0.67}$ respectively. Set space allowances were calculated using the average BW.

[b]Although this experiment did not account for differences in group size, it was included in the data analysis as it was thought that the small differences in group size would have little effect on performance.

### 4.3.4. Group Size

Most experiments report a decrease in performance as N increases (e.g. Wolter *et al.*, 2000; Hyun and Ellis, 2001). Others show little or no effect (Randolph *et al.*, 1981). However, in many experiments the effects of N, SPA and FSA are confounded (e.g., Walker, 1991; Ferguson *et al.*, 2001).

There appears to be an effect of grouping *per se* as individually housed pigs have been widely shown to outperform their group-housed counterparts (e.g., Gonyou *et al.*, 1992). The effect of increasing N on performance is therefore compared with that of individually housed pigs, assumed to be achieving their potential. Increasing N by a fixed quantity has a greater influence on smaller groups than larger ones, because the social hierarchy of small groups is disrupted to a greater degree than that of large groups which appear to lack social structure (Arey and Edwards, 1998; Turner *et al.*, 2001). A logarithmic form is used to represent this observation:

$$R_N = b_2 - g_2.\ln.(N) \qquad (4.3)$$

$R_N$ is the relative daily gain as a percentage of that of a singly housed counterpart, the constant $b_2$ is equal to 100 and $g_2$ is a scalar assumed to differ between breeds (see below). Calculated parameter values are given in Table 4.1. As group sizes greater than 10 have almost always been mixed, only experiments that allowed reasonable time periods after mixing before taking measurements were included in the analysis (Table 4.3).

The evidence for an effect of N on activity is far from clear. A trend for an increase with N has been found (Petherick, 1989; Turner *et al.*, 2002) and is included in the model. As activity represents only a small fraction of total energy requirement, the effects of N through this route are small. The increase in energy expenditure due to increased activity as N increases ($E_N$, MJ/d) is calculated as a proportion of maintenance energy ($E_{Maint}$, MJ/d) and included in the calculation of daily energy requirements. It is assumed that $E_N$ will not increase indefinitely with increasing N and so a proposed maximum is set at $N_m$. When $N < N_m$:

$$E_N = (x_1 . (N - 1)) . E_{Maint} \quad (4.4)$$

The value of $x_1$ will differ between genotypes and is discussed later. When $N \geq N_m$, $N_m$ replaces N in equation 4.

Heat production (HP, MJ/d) due to activity was reported to be between 8 and 13% of metabolisable energy intake in growing pigs (van Milgen *et al.*, 1998) equivalent to about 30 % of $E_{Maint}$. Similar values of seven to 13 % of total HP and 30 % of fasting heat production were reported by Quiniou *et al.* (2001) for group housed growing pigs. To account for a 50 % increase in activity, (an increase in $E_{Maint}$ of approximately 15%), as N increases to $N_m$, a value of 0.0075 was assigned to $x_1$ (Table 4.1). A value of 20 was assigned to $N_m$ to represent the group size beyond which $E_N$ no longer increases.

**Table 4.3.** *Data used to develop and evaluate the effect of group size on pig performance*

| Source | Average BW and BW range, kg | Group size | Space allowance, $m^2/BW^{0.67}$ |
|---|---|---|---|
| Randolph *et al.*, (1981) | 55 (20 to 90) | 5, 10, 20 | 0.045 |
| Petherick *et al.*, (1989) | 48 (40 to 56) | 6, 18, 36 | 0.049 |
| Gonyou *et al.*, (1992)[a] | 60.5 (31 to 90) | 1, 5 | 0.110, 0.080 |
| Chapple (1993)[a] | 60 (20 to 100) | 1, 3, 5 | 0.083, 0.058, 0.051 |
| Nielsen *et al.*, (1995) | 45 (34 to 56) | 5, 10, 15, 20 | 0.082 |
| Nielsen *et al.*, (1996) | 52 (39 to 65) | 1, 10 | 0.092 |
| Gonyou and Stricklin (1998)[b] | 61 (25 to 97) | 3, 5, 6, 7, 10, 15 | 0.030, 0.039, 0.048 |
| Spoolder *et al.*, (1999) | 50.5 (36 to 85) | 20, 40, 80 | 0.039 |
| Hyun and Ellis (2001)[b] | 37 (26 to 48) | 2, 4, 8, 12 | 0.080 |
| Turner *et al.*, (2001) | 42 (29 to 55) | 20, 80 | 0.080 |
| Wolter *et al.*, (2001) | 51 (6 to 116) | 25, 50, 100 | 0.043 |

[a]These experiments did not maintain constant space allowance between groups, but because space allowance was greater than the critical space allowance in all cases it was assumed that performance would not be effected.

[b]These experiments maintained a constant feeder space allowance per pen rather than per pig (1 per pen), but because group sizes were relatively small it was assumed not to affect performance.

### *4.3.5. Feeder Space Allowance*

Intake is reduced when the number of feeder spaces available to a group of pigs, falls below a critical value, ($FSA_{crit}$, feeders/pig), and continues to decrease as FSA decreases further (Nielsen *et al.*, 1995; Turner *et al.*, 2002). It is assumed that only a single pig can occupy a single feeder space at a given time. $FSA_{crit}$ is reached when all of the pigs in the group can no longer satisfy their $FI_d$ due to increased pig competition at the feeders. To try to maintain intake as FSA decreases, pigs extend their temporal pattern of feeding often into the night (Morrow and Walker, 1994) and both visit duration and feeding rate, (FR, kg/min), (Nielsen *et al.*, 1995) are increased as the number of visits decreases. $FSA_{crit}$ is therefore dependent upon N, $FI_d$ and maximum feeding rate, ($FR_{max}$, kg/min). The number of minutes in the day, 1440, is needed for consistency of units.

$$FSA_{crit} = (FI_d / (1440 \times FR_{max})). N \quad (4.5)$$

$FR_{max}$ depends upon aspects of mouth capacity (Illius and Gordon, 1987) which increases as the animal grows (Nienaber *et al.*, 1990; Nielsen, 1999), feed composition (Brouns *et al.*, 1997; Whittemore *et al.*, 2003a) and method of feed presentation. In addition the physical form in which a feed is given will be of considerable importance. It needs to be noted that the data used come only from pelleted feeds. The form relating $FR_{max}$ to BW is assumed to be:

$$FR_{max} = g_3 . BW^m \quad (4.6)$$

The parameter $m$ states how $FR_{max}$ changes with BW. A value of 1.0 is assigned to $m$ rather than 0.33 used by Illius and Gordon (1987) for ruminants, because it is mouth volume rather than incisor breadth that is relevant here. The parameter $g_3$ appropriately scales $FR_{max}$ to BW. It is assumed that neither $m$ nor $g_3$ is affected by genotype.

To test that $m = 1.0$ is a reasonable assumption, and to estimate $g_3$ for a particular feed, the results of the experiment of Walker (1991) were used. He investigated the effects on performance and feeding behaviour of pigs (37 to 90 kg) in-group sizes of 10, 20 or 30 with a single-spaced feeder supplying high quality feed and constant space allowance per pig. No differences in average daily feed intake (ADFI, kg/d) and gain (ADG, kg/d) were reported, but as expected the FR of individual pigs and the total occupancy time of the feeder increased with decreasing FSA. It was assumed that the FR reported for the largest group size of 30 was at a maximum, as FR did not increase by much when N increased from 20 to 30. The values of the parameter, $g_3$ did not change systematically as BW increased from 43 to 57 to 74 kg with a mean value of $0.788 \times 10^{-3}$ kg feed/min kg BW. The lack of change indicates that the assumption that $m = 1.0$ is a safe one.

It is expected that $FR_{max}$ will vary with feed composition and this will be reflected in the value of $g_3$. In the absence of anything better, the water holding capacity of the

feed (WHC, kg/kg), which has been shown to be a relevant descriptor for the purposes of feed intake (Kyriazakis and Emmans, 1995; Whittemore *et al.*, 2001) is used. This is supported by the data set of Whittemore *et al.* (2003a). They measured the FR of growing pigs on diets differing in WHC and found that the scaled rate of feeding was directly proportional to the reciprocal of WHC such that:

$$g_3 = 2.85 / WHC \quad (4.7)$$

Combining equations 4.6 and 4.7 gives:

$$FR_{max} = (2.85 \times BW^{1.0}) / (WHC \times 1000) \quad (4.8)$$

The WHC value for the feed used by Walker (1991) is not known. For the value of $g_3$ of $0.788 \times 10^{-3}$ kg/min kg BW, estimated from his data to be consistent with equation 7 the food would need to have a WHC value of 3.6 kg/kg. This would seem to be a reasonable estimate based on the feed composition used by Walker (1991) and values for other feeds given in the literature (Tsaras *et al.*, 1998; Whittemore *et al.*, 2001).

When FSA is limiting i.e., $FSA < FSA_{crit}$, then the constrained feed intake, $FI_c$ kg/pig, is calculated as:

$$FI_c = (1440 \times FSA \times FR_{max}) / N \quad (4.9)$$

It is assumed here that pigs do not avoid feeding immediately adjacent to one another and where troughs are used rather than individual feeders, FSA is calculated as the total number of pigs able to feed simultaneously. This is calculated from total trough width (m) and the width of the pig at the shoulders as estimated by Petherick (1983).

$$FSA = \text{Trough width} / j.\ BW^k \quad (4.10)$$

where the scalar j and exponent k are equal to 0.064 and 0.33 respectively (Petherick, 1983).

### 4.3.6. Mixing

Mixing is a transient stressor. Given sufficient time there may be no noticeable effects of mixing on performance (Spoolder *et al.*, 2000, Heetkamp *et al.*, 2002) as losses in gain due to mixing become hidden by variation. There is an initial decline in performance immediately after mixing (Tan *et al.*, 1991; Stookey and Gonyou 1994). Over time levels of performance return too normal (e.g., Tan *et al.*, 1991). Performance following mixing is depressed to a greater extent in larger animals (Stookey and Gonyou, 1994; Spoolder *et al.*, 2000) and the influence of mixing is described by:

$$R_{Mix} = b_3 - ((g_4 . BW) - ((g_5 . BW) \times \ln(t))) \quad (4.11)$$

$R_{Mix}$ is the performance (%) relative to that of a non-mixed pig, the constant $b_3$ is equal to 100, $g_4$ and $g_5$ are scalars likely to change with genotype (see below) and t is the time in days where mixing occurs on day one. At some value of t, $R_{Mix}$ will be estimated to be 100. From then on performance is normal and no longer affected by the past mixing.

In most experiments pigs are mixed to create pens of equal weight animals. In others they are mixed to create groups of diverging weights (e.g., Heetkamp *et al.*, 1995). Others again have produced mixed groups on the basis of behavioural traits (e.g., Hessing *et al.*, 1994). A further complication is that the type of building used has been shown to affect the impact of mixing on performance (Spoolder *et al.*, 2000). The apparent inconsistency in the experimental results, and the lack of data particularly for the important first few days after mixing, meant that values for the parameters in equation 4.11 could only be approximated (Table 4.1). Values were chosen so that mixing decreased performance by an average of approximately 25 % in a 70 kg pig in the first week after mixing (Tan *et al.*, 1991) and had an effect that lasted for two to three weeks (Tan *et al.*, 1991; Stookey and Gonyou, 1994).

Heetkamp *et al.* (1995) found that mixing increased the energy expenditure of pigs especially in the first few days after mixing. The increase in energy expenditure due to mixing ($E_{Mix}$, MJ/d), which decreases over time as activity levels return to normal, is added to the daily energy requirements.

$$E_{Mix} = (x_2 - (x_3 . \ln (t))) . E_{Maint} \quad (4.12)$$

The values of the parameters $x_2$ and $x_3$ change with genotype and were chosen to represent an increase in $E_{Maint}$ by a maximum of 15%, following $E_N$, and to have an effect that lasts for 2 to 3 weeks (see Table 4.1).

### *4.3.7. Incorporating effects of social stressors into a more general model*

*4.3.7.1. Information required.* The initial model used is that described in Chapter two. Information about the pig, its diet and the social and physical environments in which it is kept is needed. No additional inputs are required to describe either the thermal environment or the dietary composition. In addition to the three growth and body composition parameters an extra one is required. The inputs needed to describe the social environment are pen area ($m^2$), the number of pigs in the group, the number of feeders or trough length (m), and the occurrence or not of mixing. Up to two mixing events are allowed during a run; the weight(s) at which mixing occurs is (are) required.

*4.3.7.2. Genetic differences.* It is envisaged that there is genetic variation between pigs in their ability to cope with social stressors (Beilharz and Cox, 1967; Grandin, 1994). This is accounted for by introducing a parameter (EX) to describe the pig's ability to cope when exposed to social stressors. EX adjusts both the intensity of a stressor at which the animal becomes stressed, (e.g., $SPA_{crit}$) and the extent to which stress reduces performance and increases energy expenditure (activity) at a given stressor intensity. It is assumed in the model that these two factors are correlated, with pigs that show signs of stress earlier also being stressed to a greater degree by the same intensity of stressor. Increasing EX from zero to 10 represents a decreasing ability to cope and modifies the effect of each stressor on R by multiplying the

parameters by appropriate scaling factors (shown in Table 4.4). An EX value of five represents the mean. Because the genetic variation in pig's abilities to cope with stressors has not been formally quantified, values for the scaling factors were estimated to represent deviations of approximately one percent from the mean performance per unit change in EX. For example, EX values of zero and ten predict an approximate increase and decrease respectively in R of five percent from the mean at a given stressor intensity. $SPA_{crit}$ decreases from 0.042 to $0.031 m^2/BW^{0.67}$ as EX increases from zero to ten.

**Table 4.4.** *Scaling factors for the appropriate parameters to account for variation in ability to cope [a](EX) with social stressors*

| Space allowance | Group size | Mixing |
|---|---|---|
| $b_1 = 0.8 + 0.04EX$ | $g_2 = 0.5 + 0.1EX$ | $g_4 = 0.8 + 0.04EX$ |
| $g_1 = 0.5 + 0.1EX$ | $x_1 = 0.9 + 0.02EX$ | $g_5 = 1.033 - 0.066EX$ |
| | | $x_2 = 0.975 + 0.005EX$ |
| | | $x_3 = 1.1 - 0.02EX$ |

[a]An EX value of five represents the mean and therefore all parameters are multiplied by a scaling factor of one when EX = 5. Values were chosen to represent deviations of approximately one percent from the mean performance per unit change in EX.

*4.3.7.3. Modified potential growth.* It has been shown in studies with chicks (McFarlane *et al.*, 1989a and b) and pigs (Hyun *et al.*, 1998a and b) that the effects of stressors, at intensities expected to be found under commercial conditions, are likely to be additive rather than multiplicative, antagonistic or synergistic. It is assumed within the bounds of the model that the effects of multiple stressors on the maximum relative daily gain of the stressed animal, ($R_s$, $d^{-1}$), i.e., its decreased capacity to attain its potential, are additive and are predicted by summing the effects of the individual stressors.

$$R_s = R_p . ((100 - ((100 - R_{SPA}) + (100 - R_N) + (100 - R_{Mix}))) / 100) \quad (4.13)$$

where $R_p$ is the pigs potential relative daily gain calculated from the pigs $ADG_p$. $ADG_p$ is dependent upon the genotype and the current state of the pig.

$$R_p = ADG_p / BW \quad (4.14)$$

$R_s$ is calculated on a daily basis and used to calculate the new lower stressed maximum daily gain, $ADG_s$, which replaces $ADG_p$ in the model.

$$ADG_s = R_s \times BW \quad (4.15)$$

Predictions of the feed intake required to attain $ADG_s$, ($FI_{ds}$, kg/d), actual intake and gain are then made taking account of any changes in energy requirements due to increases in activity, $E_N$ and $E_{Mix}$, and possible constraints on intake due to limiting FSA, feed composition and the climatic environment.

## 4.4. Results

The model was used to simulate some relevant experiments with social stressors and other factors as the variables. Where model inputs are not stated the default values of the input variables are shown in Table 4.5. Other than where described below, SPA and FSA and feed bulk were always non-limiting and temperature remained thermoneutral throughout.

**Table 4.5.** *Default values of the input variables used in model predictions*

| Descriptors | Variables | Values | Descriptors | Variables | Values |
|---|---|---|---|---|---|
| [a] Pig | $P_m$, kg | 35 | Physical | Temperature, °C | 20 |
| | $L_m/P_m$, kg/kg | 2.5 | | Relative Humidity, % | 40 |
| | B, $d^{-1}$ | 0.0126 | | Air velocity, m/s | 0.15 |
| | EX | 5 | | Floor type | Concrete slats |
| Feed | DE content, MJ/kg | 14.23 | Social | Group size | 10 |
| | CP content, g/kg | 180 | | Pen area, $m^2$ | 10 |
| | CP digestibility, g/g | 0.83 | | Feeders/pen | 2 |
| | Biological Value | 0.8 | | Mixing | no |
| | [b]WHC, kg/kg | 3 | | | |
| | DM content, kg/kg | 0.88 | | | |

[a]The parameters describing the pig genotype are the growth rate parameter, B $d^{-1}$, protein weight at maturity, $P_m$ kg, the ratio of mature lipid weight, $L_m$, to $P_m$ kg/kg and ability to cope when exposed to social stressors, EX.

[b]WHC is the water holding capacity, kg/kg, used as a measure of food bulk.

### *4.4.1. Predicting the effect of space allowance and group size on time taken to grow from 20 to 50 kg*

Figure 4.1 shows the predicted time taken to grow from 20 to 50 kg when pigs are kept in varying group sizes and SPA. Group size varied between one and 100 and pen area was set at values of 0.3, 0.4, 0.5 and 0.6 $m^2$/pig. As N increased and SPA decreased, the predicted time to reach 50 kg increased. An increase in N from one to 100 increased the time taken to reach 50 kg by nine days from 40 to 49 at a SPA of 0.5 $m^2$/pig, whereas at 0.3 $m^2$/pig the time taken was increased by 10 days from 43 to 53 days. The interaction arises because $SPA_{crit}$ is reached at 21 kg in pigs given 0.3 $m^2$/pig, as opposed to 45 kg in pigs allowed 0.5 $m^2$/pig. Growth rate in the former is then limited earlier and for a longer period of time.

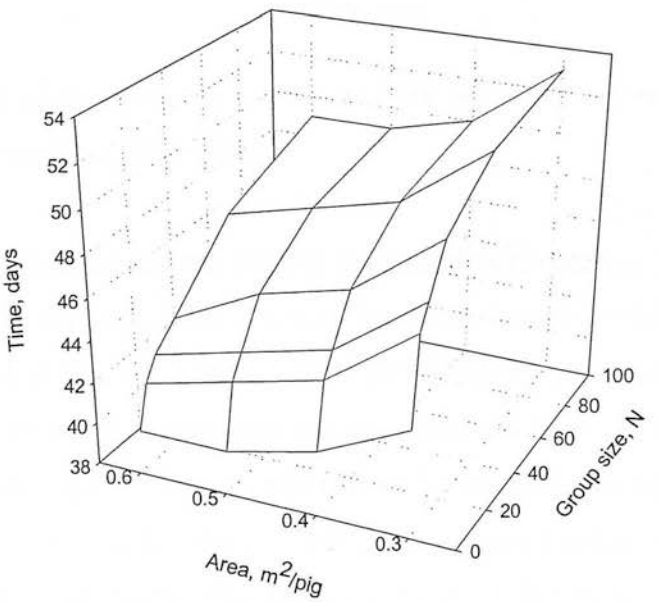


**Figure 4.1.** *Effect of pen area and group size (N) on the time taken for pigs to grow from 20 to 50 kg*

### 4.4.2. Predicting the effect of mixing at different temperatures on growth rate

The model was set up to predict the effect of mixing in 'cold' and 'hot' environments on the ADG and time taken to reach 90 kg from an initial weight of 50 kg. Temperatures were set at 5 and 28 °C for the cold and hot environments respectively and remained outside the thermoneutral zone throughout. Groups of ten pigs were either mixed or not at 60 kg. The time courses of treatment effects on ADG are shown in Figure 4.2.

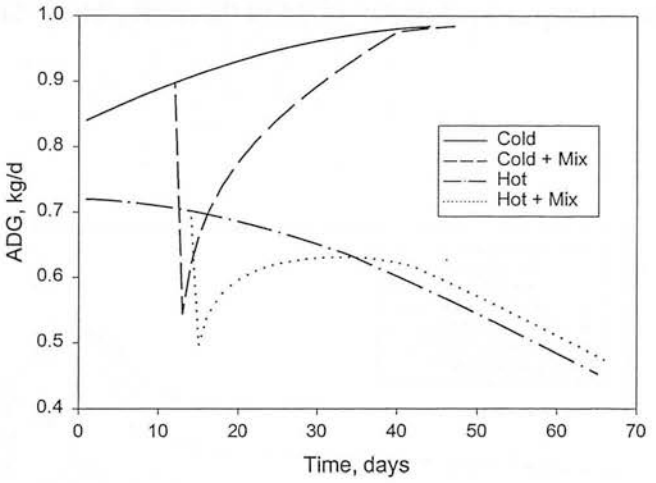


**Figure 4.2.** *The effect of mixing at cold and hot temperatures on the average daily gain of pigs grown from 50 to 90 kg*

In both hot and cold conditions mixing decreased performance. In cold conditions ADG was decreased to a greater extent immediately after mixing, -40 % (0.359 kg/d), compared to hot conditions, -29 % (0.202 kg/d). Also ADG was depressed below that of non-mixed counterparts for an additional 7 days in the cold. The ADG of pigs mixed in cold conditions returned to levels achieved by non-mixed pigs, whereas in hot conditions the ADG of mixed pigs returned to levels exceeding that of their non-mixed counterparts. This is because mixed pigs were smaller for a given age than non-mixed pigs due to their depressed ADG and as a consequence had increased upper critical, ($T_u$, °C) and lower critical temperatures. Consequently, mixed pigs in the hot treatment were less affected by heat stress than their larger non-

mixed counterparts and thus able to achieve a higher ADG. Mixed pigs in the cold treatment were able to overcome the increased extra thermal demand and maintain gain by increasing intake. As a result, mixing pigs in the hot environment increased the time taken to reach 90 kg by only one day as opposed to three days for those kept in the cold environment.

### *4.4.3. Predicting the effect of group size, pig potential and ability to cope when exposed to social stressors on pig performance*

Figure 4.3 shows the effects of ability to cope when exposed to social stressor (EX = 0, 5 or 10) on the ADG of pigs with two levels of potential performance, 'intermediate' and 'good', from 20 to 80 kg when kept in groups of between one and 100.

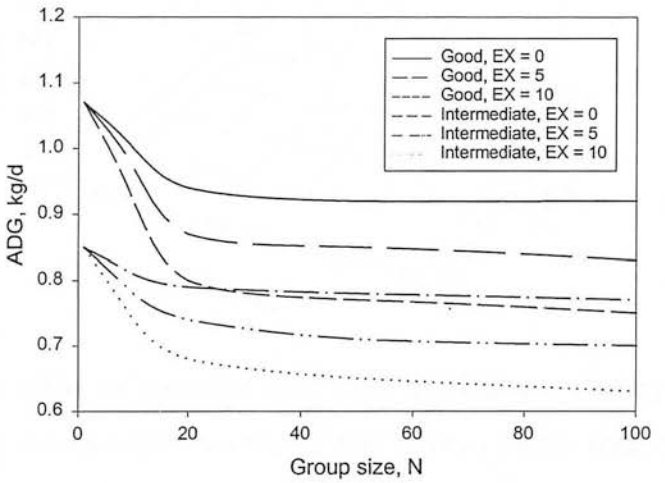


**Figure 4.3.** *The effect of group size (N), pig potential (intermediate and good) and ability to cope when exposed to stressors (EX = 0, 5 or 10) on the average daily gain of pigs grown from 20 to 80 kg*

The $ADG_p$ of the intermediate and good genotypes were 0.85 and 1.07 kg/d respectively and was achieved by increasing the growth rate parameter, B, from the default value (intermediate) to 0.016 (good). As N increased, ADG was predicted to decrease for both genotypes, with pigs with the poorest ability to cope (EX = 10)

showing the largest decrease in ADG. Pigs with EX values of ten in groups of 100 were predicted to show 8 and 16 % decreases in ADG and 4 and 7% decreases in ADFI compared to their counterparts with EX values of five and zero respectively. When N > 25, the intermediate pigs with low values of EX (EX = 0) were predicted to outperform the good pigs with high values for EX (EX = 10), having greater daily gains and intakes and reaching 80 kg two days earlier.

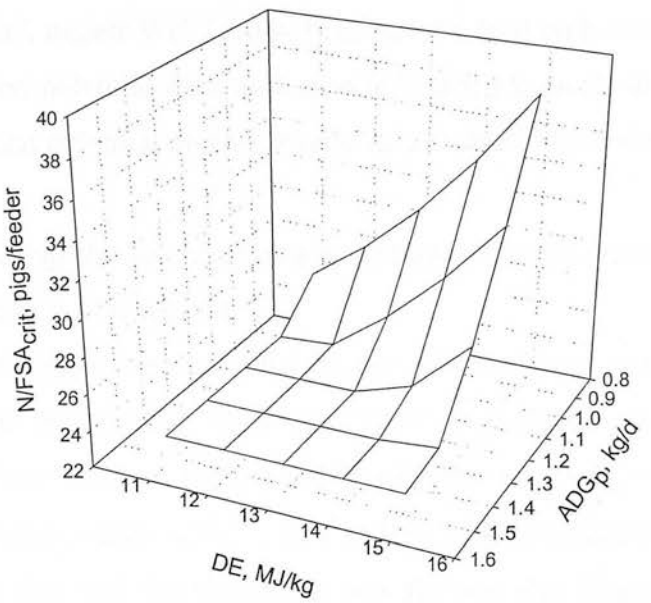


**Figure 4.4.** *The effect of potential daily gain ($ADG_p$) and dietary digestible energy (DE) content on the maximum number of pigs able to satisfy their desired feed intake per feeder space ($N/FSA_{crit}$)*

### *4.4.4. Predicting the effect of potential gain and dietary energy content on critical feeder space allowance*

The model was run to predict the effect of changing dietary digestible energy content (DEC, MJ/kg) on the $FSA_{crit}$ of pigs differing in potential at a BW of 80 kg. Five pig genotypes were simulated to have $ADG_p$ values ranging from 0.85 to 1.53 kg/d at 80 kg. This was achieved by increasing B in the model. The model was run using five feeds decreasing in one MJ intervals from 15 to 10 MJ DEC/kg. In reality this may be achieved by diluting the feed with a low energy material such as wheat bran (WB)

(from 0 to 86%). This would increase the WHC from 3.5 to 4.6 kg/kg following the equation used by Whittemore *et al.* (2003b), WHC = 3.5 + (0.013.WB). The remaining feed descriptors were kept constant. Results from the simulations are shown in Figure 4.4. The maximum number of pigs able to satisfy their $FI_d$ per feeder space, $N/FSA_{crit}$, is predicted to increase as $ADG_p$ decreases and DEC increases. Values predicted for $N/FSA_{crit}$ ranged from 23.6 for pigs with the highest potential on the lowest DEC feed to 37.9 for pigs with the lowest potential on the highest DEC feed. This is because $FI_d$ decreases as $ADG_p$ decreases and DEC increases. $N/FSA_{crit}$ is predicted to remain constant for the higher potential pigs on the lower DEC, higher WHC feeds, because of a feed bulk constraint on intake. Pigs with the lowest potential were able to satisfy their $FI_d$ on all five feeds, whereas pigs with the highest potential pigs were only able to fulfil $FI_d$ on the highest energy feed.

### *4.4.5. Predicting the effect of space allowance, temperature and genotype on pig performance at a weight*

The effect of temperature and SPA on the ADG of three genetic lines of pigs was predicted. The three genetic lines were 'poor' ($B = 0.01$, $P_m = 33$, $L_m/P_m = 3$, EX = 2), 'intermediate' (default values) and 'good' ($B = 0.014$, $P_m = 38$, $L_m/P_m = 2$, EX = 8), and had $ADG_p$ values of 0.77, 0.98 and 1.11 kg/d respectively. The pigs weighed 60 kg at the start and the simulation was for one day. Pen area was increased in increments of 0.1 $m^2$/pig from 0.3 to 0.8 $m^2$/pig, giving SPA values between 0.019 to 0.047 $m^2/BW^{0.67}$, and temperature was increased in 5 deg C intervals from 0 to 30 °C. ADG was predicted to decrease as temperature increased above the $T_u$, and as SPA fell below $SPA_{crit}$. Decreases in ADFI and ADG of 61 and 48 % respectively were predicted for the good genotype pig kept at 0.3 $m^2$/pig and 30 °C compared to one at 0.8 $m^2$ and 0 °C. The equivalent predicted decrease in ADFI and ADG for the poor genotype was 56 % and 40 % respectively. The reason for the greater decline in ADFI and ADG in the good genotype is because the $T_u$ is predicted to be lower and $SPA_{crit}$ is predicted to be higher, due to an enhanced growth rate and poorer ability to cope when exposed to social stressors respectively. The $T_u$ was predicted to be 22, 25 and 26 °C and $SPA_{crit}$, 0.64, 0.61 and 0.56 $m^2$/pig for the good, intermediate and poor genotypes respectively.

## 4.5. Discussion

The influence of social stress on pig performance, although undeniable, is frequently underestimated and in pig growth modelling generally ignored. Black (2002) noted that 'current pig models do not predict well the effects of stress encountered by pigs reared in commercial environments'. The aims here were to describe and quantify the effects of the major social stressors on the performance of growing pigs and to incorporate these relationships into the pig growth simulation model described in Chapter two. The adapted model described here is an initial attempt at quantifying and predicting the effects of the major social stressors on the intake and gain of different genotypes of pigs.

The conceptual equations between the social stressors and pig performance described here were derived, where possible, on biological grounds rather than by using some polynomial regression technique to fit data (e.g., Kornegay and Notter, 1984 and Turner *et al.*, 2003). To at least some extent this allows the problems of using a strictly empirical approach to be avoided, and effects may be able to be interpreted biologically. For example the equations of Kornegay and Notter (1984) and Turner *et al.* (2003) predict an ADG of zero when group size reaches 338 and 1363 respectively in growing pigs. This seems unrealistic as pigs in groups of up to 2000 are now kept in profitable pig production enterprises, but is rather a consequence of the range of data used in the empirical analysis. Incorporating equations such as those developed here into a more general model allows any interactions that exist between the type of pig and its environment to be predicted, and is an improvement over simply altering output parameters by an empirical adjustment.

Integrating the derived equations into a growth model poses the problem of describing how social stressors affect pig performance. Detailed experiments where not only intake and gain are measured, but also body composition and physiological parameters relating to stress and the control of growth, are required to quantify the underlying biological mechanism responsible for stressor effects (Morgan *et al.*, 1999). Until evidence is available to help elucidate the exact mechanism(s), a

decrease in the animal's capacity to attain its potential, is used here to represent the mechanism responsible for the decreased performance of socially stressed animals. This is in preference to other potential mechanisms, such as increased metabolic demands diverting resources from the growth process (Elsasser *et al.*, 2000) or a direct reduction in appetite (Matteri *et al.*, 2000).

A decrease in the animal's capacity to attain its potential is the mechanism that is chosen because it allows the desired intake of the stressed animals, $FI_{ds}$, to be predicted in a simple way. This, in turn, makes the task of incorporating the mechanism into the growth model easier, and is consistent with the experimental evidence, including that of Chapple (1993). $FI_{ds}$, is predicted directly from the animals depressed potential as opposed to first determining the non-stressed appetite (intake), $FI_d$, from which $FI_{ds}$ is calculated. This latter method is used when a direct reduction in appetite is employed as the mechanism, such as in the enriched theory of food intake regulation by Kyriazakis (2003). Chapple (1993) used the AUSPIG simulation model of Black *et al.* (1986) to investigate how changes induced by social stressors observed in experiments, including increases in body lipid percentage, may come about. He found that the experimental observations could not be explained by a reduction in intake alone, i.e., a direct reduction in appetite, but required instead a reduction in the pig's ability to 'deposit body tissue'. Experiments where an increased protein supply to crowded pigs did not overcome their decreased performance relative to non-crowded pigs (NCR-89, 1993; Edmonds *et al.*, 1998; Ferguson *et al.*, 2001) also support the chosen mechanism. Although there is some circumstantial evidence that a decrease in the animal's ability to attain its potential is the responsible mechanism, the underlying cause at the physiological level is not clear. It has been suggested that physiological factors such as growth hormone (MacRae and Lobley, 1991), plasma cortisol (Von Borell *et al.*, 1992), insulin-like growth factor and cytokines (Chapple, 1993) may be responsible for directly down-regulating tissue growth. Further work to quantify how the mechanism may operate is required.

For the model to be used to make predictions, accurate descriptions of the social and physical environment, feed composition and pig genotype are needed. Some of the inputs e.g., group size, feeder space, floor type, and dietary energy and protein contents are relatively easy to obtain. Accurate descriptions of the genotype, including a description of the pigs potential (Knap *et al.*, 2002) and ability to cope when exposed to stressors, EX, are more difficult to obtain. As the parameter EX reflects a newly introduced concept, there is currently no means of assigning an accurate estimation of its value to a particular genotype. However, assuming that there is a measurable phenotypic difference between types of pigs it is thought that genetic characterisation is possible. The work of de Greef *et al.* (2003) and Kanis *et al.* (2003) supports this. They described and evaluated a conceptual framework for breeding for improved welfare in pigs and showed that it is possible to select for abilities to cope with stressors such as environmental temperature. To fully describe a particular pig's genetic potential a concise set of model parameters are required (Knap *et al.*, 2002). In the model used here they are the mature protein mass, $P_m$, the ratio of lipid to protein at maturity, $L_m/P_m$ and a growth rate parameter, B. Although these parameters are not universally regarded as the most suitable descriptors of potential growth (e.g., Schinckel and de Lange, 1996), they have much support (Ferguson *et al.*, 1997; Whittemore and Green 2002; Pomar *et al.*, 2003). Methods to characterise them have been suggested by Ferguson and Gous (1993) and Knap *et al.* (2002).

Validating models is a difficult process, as no model can be validated in any general way and any apparent invalidation will always be subjective (Black, 1995). Furthermore, suitable experimental data to enable sensible comparisons with model predictions of multiple interactions are almost non existent. An exception is Hyun *et al.*, (1998a and b) who investigated the effects of combinations of SPA, temperature and mixing on pig performance but as the resulting data were used in the estimation of parameter values they cannot be used for model testing.

While the model here cannot be validated, its performance can be evaluated. Quantitatively, predictions made by the functional forms are in good agreement with previous attempts to quantify social stressor effects. The model predicts a decrease in performance of approximately 7.5 % over a change in SPA from 0.039 to 0.030 $m^2/BW^{0.67}$. This compares with a 10 % decrease in performance predicted by Black *et al.* (1995) over the same range. It is expected that there is no effect of SPA when SPA > 0.039, and therefore the 10 % decrease in performance over the range of 0.048 to 0.031 $m^2/BW^{0.67}$ suggested by Whittemore (1998) also compares favourably. Although the empirical equations of Kornegay and Notter (1984) and Turner *et al.* (2003) have their limitations as discussed above, they are the only sources available for comparing the effects of group size on performance. As N increased from three, the minimum range for the equations of Kornegay and Notter (1984) and Turner *et al.* (2003), to their maximum ranges of 33 and 120 respectively, a decrease in ADG of 9 and 8.6 % is predicted for growers. This compares to the model predictions of 9.2 and 14.1 % over the same ranges. The effects of FSA and mixing have not been considered in equations elsewhere and so no comparison is possible. However, $FR_{max}$ predicted by the model compares well with experimental data of Nielsen *et al.* (1995). They measured $FR_{max}$ for 42 kg pigs, kept in groups of 20, to be 31.6 g/min which compares to the value of 34.2 g/min predicted by the model when a realistic value for WHC of 3.5 is used.

When estimating the values of the parameters in the conceptual equations many assumptions had necessarily to be made. For example, when predicting the effect of FSA on intake, it was assumed that there was a 24-hour feeding period, no feed wastage, a non-limiting rate of feed supply and that all pigs were constrained equally when FSA became limiting. It was also assumed that one pig immediately succeeded another at the feeder. The assumption that all pigs were equally constrained highlights one of the problems, and perhaps the main limitation of using a model that represents the single, average pig. In reality not all of the individual animals will be affected equally when exposed to the same stressors. For example, in established groups dominant pen mates may chronically stress others while remaining relatively

unaffected causing some animals to decrease their intake long before others (Nielsen, 1999).

To account for individual differences within a group, a population model is required and this is a sensible next stage of model development. In addition to accounting for differences in individual $ADG_p$, as is the case in the models of Knap (2000) and Pomar *et al.* (2003), differences in ability to cope when exposed to stressors are also required. While these individual differences may be difficult to quantify, genetic characterisation is an area where much work is still needed, the model described here provides a framework that is capable of dealing with these differences. The parameter EX, used to account for differences in responses to social stressors, may be used as the starting point for modelling individual pig differences, with individual animals of a group being assigned varying values around the group mean. There is evidence that selecting for increased lean in pigs has indirectly selected for aggression (van Erp-van der Kooij *et al.*, 2000) and this may be one way of assigning EX parameter values to individuals, with leaner pigs assumed to be affected to a greater degree by stressors. This would assume that ability to cope and aggressiveness are negatively correlated which may not be the case. It should be noted that not only will individuals react differently to the environment, but also they will be influenced by others, and in turn influence them (Muir and Schinckel, 2002). One of the advantages of extending a model of an individual to a population, as discussed above, is that such effects can be accounted for.

# Chapter 5

## Modelling the effects of environmental stressors on the performance of populations of pigs

## 5.1. Abstract

To investigate the impact of between-animal variation on population responses, a simulation model of pig growth that predicts the effect of the social, physical and nutritional environments on pig food intake and performance was extended to deal with individual variation. Variation was generated in initial state, potential growth and ability to cope when exposed to social 'stressors' (EX). Variation in initial state is described by initial body weight ($BW_0$) from which the chemical composition of the pig is calculated. Variation in potential is described by creating variation in the three genetic growth descriptors. Variation in EX exists between genotypes, where it has been suggested that leaner, more modern genotype pigs tend to be less able to cope. It is expected that within a population or group that the social environment, i.e., group composition and social hierarchy, also affects an individuals ability to cope. In the model, it is assumed that the larger, more dominant individuals are better able to cope when exposed to social stressors. Consequently, within a population, EX is correlated with body weight around the genotype mean. Model predictions show that increasing the variation in $BW_0$ and EX increases the variation in pig performance. This is an important practical consideration in commercial pig production where the homogeneity of the population at the target slaughter weight affects the economical efficiency of an enterprise. The way a stressor constrains performance determines whether the mean population response to a particular stressor is the same as the average individual response. If all pigs are affected at the same stressor intensity, e.g., all pigs in a group are either mixed or not, then the predicted average individual and mean population responses will be the same. If however, the intensity of stressor at which performance becomes limiting is able to differ between individuals, such as space allowance or temperature, then differences between the individual and mean population responses will be predicted. Variation in the growth response of a population was determined to a greater extent by variation in EX and $BW_0$ than by variation in growth potential, when pigs were housed in simulated conditions likely to be encountered in commercial environments. Consequently, decreasing the variation in $BW_0$ and improving pig's ability to cope may be a better way of improving pig performance than selecting for increased potential *per se*.

## 5.2. Introduction

Models intended to simulate animal performance typically represent a single animal. They have been developed for poultry (e.g., Emmans, 1981), cattle, (e.g., Williams and Jenkins, 2003), sheep (e.g., Black, 1974; Blaxter *et al.*, 1980), dairy cows (e.g., Baldwin *et al.*, 1987) and growing pigs (e.g., Whittemore and Fawcett, 1976; Black *et al.*, 1986; Pomar *et al.*, 1991; Bridges *et al.*, 1992). The assumption necessarily made is that the response of the population will be the same as that of the deterministically simulated response of the 'average' individual. This will be the case only if all animals in the population have an equal growth potential, all are at the same stage of growth and all react in the same way to encountered stressors. However, due to between-animal variation there may be differences between the response of the average individual and the mean response of the population, which is an average of all individuals (Fisher *et al.*, 1973; Ferguson *et al.*, 1997). In order to attempt to predict adequately the response of a population in a given environment it is necessary to take account of between animal variation (Emmans and Fisher, 1986).

The stochastic growth models of Ferguson *et al.* (1997), Knap (2000a) and Pomar *et al.* (2003) predict the mean population response by taking the average of the simulated individual pig responses. These models deal only with variation in potential growth. Any variation that may exist between individuals in initial state and ability to cope when exposed to social factors that may act as stressors e.g., group housing and mixing, is ignored. Even under the best experimental conditions, there is likely to be variation in initial state between pigs at the start of the trial period. This needs to be accounted for as the homogeneity of a group in terms of initial weight may affect the homogeneity of the group, and hence profitability at slaughter. Genetic variation may exist between populations in their mean response to environmental stressors (Beilharz and Cox, 1967) and it has been suggested that leaner, modern genotypes tend to be less able to cope (Grandin, 1994; Torrey *et al.*, 2001). It is expected that variation in ability to cope exists within populations and that group composition and the individual's position within the social hierarchy affects the ability of an individual to cope in a given social environment.

The starting point of this Chapter was the pig growth model described in Chapter four that predicts the effect of the social, physical and nutritional environment on pig performance. The objective was to extend the model so that it could deal with between-animal variation and to investigate the impact of individual variation in potential growth, initial state and ability to cope when exposed to environmental stressors on performance. Variation between individuals in their initial state and ability to cope when exposed to social stressors has been ignored in previous models.

## 5.3. Materials and methods

### *5.3.1. Model description*

The individual pig growth model described in Chapter two was extended to include the effect of social stressors on individual pig performance in Chapter four. Here it is further developed to predict the effect of between-animal variation. The theory behind the model is described below.

The individual pig is described by four genetic parameters. Three of these are used to predict its potential for growth: protein weight at maturity ($P_m$, kg), the ratio of lipid to protein at maturity ($L_m/P_m$, kg/kg) and a growth rate parameter (B, $d^{-1}$). The fourth parameter describes the ability to cope when exposed to social stressors (EX). The initial state of the pig is described by initial body weight ($BW_0$, kg) from which the chemical composition of the pig is calculated assuming the pig has its ideal composition set by its genotype. Pig genotype and current protein weight only determine the potential rate of protein retention ($PR_{max}$, kg/d). Its value is used to determine the potential gains of the other chemical components (Emmans, 1988; Emmans and Kyriazakis, 1997). Potential average daily gain ($ADG_p$, kg/d) is the sum of the potential gains of the chemical components; gut fill is assumed to be five percent of the gain.

It is assumed that all pigs will attempt to consume an amount of feed that will satisfy their energy and protein requirements for $ADG_p$, maintenance and any compensatory lipid gain as described in Chapter two. The amount of feed that allows this to be achieved is termed desired feed intake ($FI_d$, kg/d) and is calculated from the

composition of the given feed. Any costs of thermoregulation are calculated separately and any increase in requirements from exposure to pathogens is ignored. The only feed resources considered are energy and protein; any of the essential amino acids may be first limiting. Actual feed intake and the consequent actual gains in chemical component weights, are predicted taking into account the capacity of the animal to consume feed bulk, its ability to maintain thermoneutrality and consequences of the social environment. Gains of the chemical components are calculated by partitioning the energy and ideal protein supplies above maintenance between protein (PR, kg/d) and lipid (LR, kg/d) retention according to Kyriazakis and Emmans (1992a and b).

The physical environment is described by the ambient temperature, air velocity, floor type and relative humidity and these set the maximum ($HL_{max}$, MJ/d) and minimum, ($HL_{min}$, MJ/d) heat losses in the given environment. A comparison with the pig's calculated heat production (HP, MJ/d) determines whether the pig is hot ($HP > HL_{max}$), cold ($HP < HL_{min}$) or thermoneutral ($HL_{min} < HP < HL_{max}$). A constraint on intake will operate in hot environments due to an inability to lose the heat produced by maintenance and growth to the surrounding environment. In cold environments, there is an extra thermal demand placed upon the pig. If conditions are thermoneutral, no further action is taken.

The social environment is described by group size (N), pen area (A $m^2$), feeder space allowance, (FSA, either as feeder spaces/pig or m/pig), and the occurrence or not of mixing. The effective space allowance (SPA, $m^2/BW^{0.67}$) is calculated from N, A and body weight (BW, kg). All of these factors may act as social stressors and it is assumed in the model that they decrease performance by lowering the capacity of the animal to attain its potential following Emmans (1981) and Chapple (1993). The exception is FSA that directly constrains intake when limiting. The descriptor EX adjusts both the intensity of the stressor at which the pig becomes stressed and the extent to which each stressor reduces performance at a given stressor intensity. It is assumed in the model that these two factors are perfectly correlated; pigs that show signs of stress at a lower stressor intensity are also stressed to a greater degree at any

given stressor intensity. Increasing the value of EX represents a decreasing ability to cope when stressed. The model was calibrated so that a unit change in EX produced deviations of approximately one percent from the mean performance.

The model can be run either to a final BW ($BW_f$, kg) or for a given time period (t, days). For a complete description of the model including inputs, see Chapters two and four.

### *5.3.2. Creating a population*

*5.3.2.1. Genetic characteristics.* The potential growth of individuals within a population can be described by generating variation around the population means of each of the genetic parameters, B, $P_m$ and $L_m/P_m$. (Emmans, 1989; Ferguson *et al.*, 1997). Between animals of the same population there is likely to be a negative correlation between B and $P_m$ (Emmans, 1988; Knap, 2000a; Lewis *et al.*, 2002). The scaled rate parameter, $B^* = B.P_m^{0.27}$, described by Emmans and Fisher (1986) is used as an alternative to B to avoid the problems caused by the correlation between B and $P_m$. The values of $B^*$, $P_m$ and $L_m/P_m$ are assumed to be uncorrelated and normally distributed (Ferguson *et al.*, 1997; Knap 2000a; Pomar *et al.*, 2003).

*5.3.2.2. Initial state.* Individual variation in $BW_0$ is generated from the assigned genotype mean, ($\mu BW_0$, kg) and standard deviation ($\sigma BW_0$, kg) of $BW_0$ using the simulated genetic parameters of the individual to correlate $BW_0$ with potential growth. By this means individuals in the group with the greatest potential will tend to have the highest $BW_0$ as would be expected from non-limiting growth. The initial weight of pig *i*, ($BW_{0i}$, kg) was calculated as:

$$
\begin{aligned}
BW_{0i} = {} & \mu BW_0 \\
& + a.\,(b_4.(1 - (\mu B^* / B^*_i)).(\sigma BW_0.(\mu B^* / \sigma B^*)) \\
& + b_5.(1 - ((\mu L_m/P_m) / (L_m/P_{mi})).(\sigma BW_0.((\mu L_m/P_m) / (\sigma L_m/P_m)) \\
& + b_6.(1 - (\mu P_m / P_{mi})).(\sigma BW_0.(\mu P_m / \sigma P_m))) \\
& \pm \text{residual}_i \qquad \text{(kg)} \qquad (5.1)
\end{aligned}
$$

The parameters $B^*_i$, $P_{mi}$ and $L_m/P_{mi}$ are the genetic parameter values for pig *i*. The parameters $\mu B^*$, $\mu P_m$ and $\mu L_m/P_m$ are the mean values and $\sigma B^*$, $\sigma P_m$ and $\sigma L_m/P_m$ the standard deviations of $B^*$, $P_m$ and $L_m/P_m$ respectively. The parameter *a* is a scaling factor, with a value chosen to generate expected values, and the parameters $b_4$, $b_5$ and $b_6$ determine the degree of correlation between $BW_{0i}$ and $B^*_i$, $L_m/P_{mi}$ and $P_{mi}$ respectively. The value of $residual_i$ is drawn at random from a normal distribution with a mean value chosen to account for the expected variation in $BW_0$. It adds a non-genetic component to $BW_{0i}$. The initial chemical composition of each pig is calculated from $BW_{0i}$ assuming it has its ideal body composition ,as determined by its genotype, at the start of the trial period. In this way, at the same $BW_0$ genetically fatter pigs (higher values for $L_m/P_m$) will have a lower initial protein weight (P, kg) and a higher initial lipid weight (L, kg) than genetically thinner pigs.

*5.3.2.3. Ability to cope.* It is assumed in the model that there is a negative correlation between $BW_0$ and EX. Individual values for EX ($EX_i$) are generated around the assigned genotype mean ($\mu EX$) and standard deviation ($\sigma EX$) of EX, whilst being negatively correlated to $BW_0$. This results in a normally distributed population of EX, with pigs with the highest $BW_0$ tending to have the lowest values for EX.

$$EX_i = \mu EX + b_7.((1 - (BW_{0i} / \mu BW_0)).(\sigma EX.(\mu BW_0 / \sigma BW_0))) \pm residual_i \qquad (5.2)$$

The parameter $b_7$ determines the degree of correlation between $BW_0$ to EX and is equal to one. The $residual_i$ is drawn at random taking account of $\sigma EX$. Within a population, EX is not directly correlated to leanness. However, leaner animals will tend to have higher EX values due to the positive correlation between $L_m/P_m$ and $BW_0$ (equation 5.1) and the negative correlation between $BW_0$ and EX (equation 5.2). Between populations, it is expected that modern, 'leaner', genotypes will have higher values of EX than traditional, 'fatter', genotypes (Grandin, 1994; Torrey *et al.*, 2001; Schinckel *et al.*, 2003). A value of ten represents the mean response for the average pig type (changed from five in Chapter four). It is expected that $5 \leq \mu EX \leq$

15 and $\sigma EX \leq 2.5$ are conditions that will hold for all populations to avoid problems of generating non-positive values for $EX_i$.

*5.3.2.4. Drawing individual pigs.* For each simulated pig within a population, values for $B^*_i$, $P_{mi}$ and $L_m/P_{mi}$ are drawn at random from a normally distributed population using the estimated means and coefficients of variation to ensure that no correlation exists between them (Ferguson *et al.* 1997; Knap 2000a; Pomar *et al.* 2003). Values for $BW_{0i}$ and $EX_i$ are then generated from their respective means and standard deviations (model inputs) whilst taking into account the generated genetic parameter values of the individual (equations 5.1 and 5.2). The values that characterise each animal are drawn before each simulation run and are able to be maintained for multiple simulation runs.

### 5.3.3. Simulations

The model was used to simulate some relevant experimental conditions with environmental stressors as the variables. Particular attention is given to the social stressors. The genetic line of van Lunen (1994) as characterised by Knap (2000b) was used in all model simulations. The estimated means and coefficients of variation (shown in brackets) for the parameters that determine the potential growth of the pig, $B^*$, $P_m$ and $L_m/P_m$ were 0.0408 (0.03), 32.0 (0.07) and 1.2 (0.15) respectively. These values were kept constant throughout all model simulations.

**Table 5.1.** *Default values of the input variables used in model predictions*

| Descriptor | Variables | Values | Descriptor | Variables | Values |
|---|---|---|---|---|---|
| [a]Pig | Modern genotype | | Physical | Temperature, °C | 20 |
| Feed | DE content, MJ/kg | 14.2 | | Relative Humidity, % | 40 |
| | CP content, g/kg | 180 | | Air velocity, m/s | 0.15 |
| | CP digestibility, g/g | 0.83 | | Floor type | Concrete slats |
| | Biological value | 0.8 | Social | Group size | 20 |
| | [b]WHC, kg/kg | 3.0 | | Pen area, $m^2$ | 20 |
| | DM content, kg/kg | 0.88 | | Feeders/pen | 2 |
| | | | | Mixing | No |

[a]the genotype characterised by Knap (2000b) was used in all model simulations. For details of the parameter values see text. [b]WHC is the water holding capacity of the feed used as a measure of bulk.

Where model inputs are not stated below the default values of the input variables used are those shown in Table 5.1. Other than where described, SPA, FSA and feed bulk are expected to be non-limiting and the temperature thermoneutral for the average animal. In all simulations, 500 animals were drawn at random. Group sizes of 20 were used in all simulations, except where the effect of N was investigated. Therefore using 500 pigs is equivalent to simulating 25 replicates of 20 pigs. The simulated phenotypic variation predicted results from interactions between the generated variation of the individual pigs and the thermal, dietary and social environments in which they are kept.

*5.3.3.1. The effect of variation in initial body weight ($BW_0$) and ability to cope with social stressors (EX) on pig performance.* The effect of variation in $BW_0$ and EX on the variation in t for all individuals to reach a given $BW_f$ (set $BW_f$ simulation) and the variation in $BW_f$ over a given number of days (set t simulation) was predicted. Variation in average daily gain (ADG, kg/d), average daily feed intake (ADFI, kg/d) and body composition were also predicted. The weight range used is that of a typical finisher system from 60 to 100 kg. Pigs were mixed at 75 kg and kept with an area of 0.7 $m^2$/pig. In the model, this space allowance becomes limiting at about 75 kg, coinciding with the occurrence of mixing. The number of days used in the simulations with a set period of time was the average number of days predicted to grow from 60 to 100 kg in the set weight simulations, t = 50 days. Variation was generated in $BW_0$ by increasing $\sigma BW_0$ from zero to ten kilograms in two-kilogram intervals, with $\sigma EX = 0$, and in EX by increasing $\sigma EX$ from zero to 2.5 in half unit intervals, with $\sigma BW_0 = 0$. A value of ten for $\mu EX$ was maintained throughout. Variation was also generated in $BW_0$ and EX simultaneously. In one case values of 6 and 1.5 were used for $\sigma BW_0$ and $\sigma EX$ respectively. In another, the effects of increasing $\sigma BW_0$ and $\sigma EX$ to 10 and 2.5 respectively were simulated.

*5.3.3.2. Comparison of the average pig response with the mean population response.* The model was used to predict the response of the average individual in the population and the mean population response. The same 500 pigs ($\mu EX = 10$ and $\sigma EX = 1$) were used in each simulation, and the mean population response compared

to that of the average pig, i.e., zero variation. The effects of four social stressors at differing intensities were simulated. (i) Group size was increased from one to 100 with a simulation interval from 20 ($\sigma BW_0 = 1$) kg to 60 kg. (ii) Space allowance was reduced by decreasing pen area in 0.02 $m^2$ intervals from 0.80 to 0.40 $m^2$/pig. The simulation period was for one day, and $\mu BW_0$ and $\sigma BW_0$ were set at 60 and 4 kg respectively. (iii) Mixing either occurred or not on day one and the simulation period was from 60 kg ($\sigma BW_0 = 4$ kg) to 100 kg. (iv) Temperature was increased from 20 to 30 °C in one degree intervals. The simulation period was for one day, and $\mu BW_0$ and $\sigma BW_0$ were set at 60 and 4 kg respectively.

## 5.4. Results

### *5.4.1. The effect of variation in initial body weight ($BW_0$) and ability to cope with social stressors (EX) on pig performance*

Tables 5.2 and 5.3 show the predicted effect of within population variation in EX and $BW_0$ on the performance of growing pigs over a given weight range and time period respectively. As variation in $BW_0$ and EX increases, variation in both t (set $BW_f$ simulations) and $BW_f$ (set t simulations) increase, whilst the mean population responses remain unchanged. At zero variation in $BW_0$ and EX all pigs have the same $BW_0$ and ability to cope and so all of the variation in performance is a result of differences between pigs in their potential only. This case is shown in the first line of Tables 5.2 and 5.3. The standard deviation of t ($\sigma t$, days) increased from 3.93 to 14.23 days as $\sigma BW_0$ was increased from zero to ten kilograms. For the same increase in $\sigma BW_0$, the value of $\sigma BW_f$ increased from 2.85 to 11.02 kg. As $\sigma EX$ was increased from zero to 2.5, $\sigma t$ increased from 3.93 to 5.52 days and $\sigma BW_f$ from 2.85 to 4.13 kg.

Mean values of 0.80 and 2.17 kg/d were predicted for ADG and ADFI respectively and were not affected by increasing $\sigma BW_0$ and $\sigma EX$. Variation in ADFI increased with increasing variation in both $BW_0$ and EX, whereas variation in ADG increased only with increasing variation in EX. The mean final body composition, as weights of L and P, was not affected by increasing $\sigma BW_0$ and $\sigma EX$. Variation in P and L was predicted to increase with increases in $\sigma BW_0$ and $\sigma EX$ only in the set time

simulations. Simultaneously generating variation in $BW_0$ and EX affected variation in the performance parameters in a non-additive manner (Tables 5.2 and 5.3).

**Table 5.2.** *Effect of variation in initial BW ($BW_0$, kg) and ability to cope (EX) on the time taken (t, days) to reach 100kg from a mean $BW_0$ of 60 kg. ADG, ADFI, P and L are the average daily gain, average daily feed intake, protein content and lipid content respectively. Mixing occurred at 75 kg and pigs were given a space allowance of 0.7 $m^2$/pig throughout*

| [a]$BW_0$, kg | [b]EX | t, days | ADG, kg/d | ADFI, kg/d | P, kg | L, kg |
|---|---|---|---|---|---|---|
| 60.0 (0.00) | 10.0 (0.00) | [c]50.7 (3.93) | [c]0.80 (0.060) | [c]2.17 (0.104) | [c]17.78 (0.352) | [c]15.59 (1.534) |
| 60.1 (2.07) | 10.0 (0.00) | 50.8 (5.48) | 0.80 (0.057) | 2.17 (0.107) | 17.78 (0.333) | 15.59 (1.445) |
| 60.2 (4.19) | 10.0 (0.00) | 51.5 (7.64) | 0.80 (0.056) | 2.17 (0.119) | 17.78 (0.357) | 15.59 (1.592) |
| 59.9 (5.74) | 10.0 (0.00) | 51.5 (9.42) | 0.80 (0.052) | 2.16 (0.121) | 17.78 (0.358) | 15.58 (1.544) |
| 58.7 (7.87) | 10.0 (0.00) | 52.2 (11.59) | 0.80 (0.053) | 2.16 (0.131) | 17.77 (0.346) | 15.63 (1.500) |
| 59.1 (10.04) | 10.0 (0.00) | 52.2 (14.23) | 0.79 (0.054) | 2.15 (0.132) | 17.78 (0.338) | 15.60 (1.506) |
| 60.0 (0.00) | 10.2 (0.47) | 50.79 (4.06) | 0.80 (0.061) | 2.17 (0.105) | 17.76 (0.350) | 15.70 (1.548) |
| 60.0 (0.00) | 10.3 (0.94) | 50.79 (4.16) | 0.80 (0.063) | 2.17 (0.108) | 17.79 (0.359) | 15.54 (1.580) |
| 60.0 (0.00) | 10.3 (1.45) | 50.79 (4.71) | 0.80 (0.072) | 2.17 (0.117) | 17.79 (0.342) | 15.61 (1.495) |
| 60.0 (0.00) | 10.2 (1.93) | 50.79 (5.14) | 0.80 (0.079) | 2.17 (0.128) | 17.77 (0.349) | 15.64 (1.579) |
| 60.0 (0.00) | 9.9 (2.53) | 50.79 (5.52) | 0.80 (0.087) | 2.17 (0.140) | 17.79 (0.354) | 15.53 (1.576) |
| 59.3 (5.77) | 10.1 (1.40) | 52.1 (11.48) | 0.80 (0.071) | 2.17 (0.161) | 17.77 (0.331) | 15.63 (1.435) |
| 59.1 (10.39) | 10.1 (2.42) | 53.2 (18.83) | 0.80 (0.085) | 2.17 (0.212) | 17.77 (0.328) | 15.61 (1.483) |

[a,b] Simulated values for [a]$\mu BW_0$ and ($\sigma BW_0$) and [b]$\mu$EX and ($\sigma$EX) respectively. [c]Result of variation in growth potential only.

**Table 5.3.** *Effect of variation in initial BW ($BW_0$, kg) and ability to cope (EX) on the final BW ($BW_f$, kg) achieved after a simulation period of 50 days from a mean $BW_0$ of 60 kg. ADG, ADFI, P and L are the average daily gain, average daily feed intake, protein content and lipid content respectively. Mixing occurred at 75 kg and pigs were given a space allowance of 0.7 $m^2$/pig throughout*

| [a]$BW_0$, kg | [b]EX | $BW_f$, kg | ADG, kg/d | ADFI, kg/d | P, kg | L, kg |
|---|---|---|---|---|---|---|
| 60.0 (0.00) | 10.0 (0.00) | [c]100.2 (2.85) | [c]0.80 (0.057) | [c]2.17 (0.113) | [c]17.74 (0.475) | [c]15.53 (1.612) |
| 60.0 (2.17) | 10.0 (0.00) | 100.0 (4.23) | 0.80 (0.056) | 2.17 (0.137) | 17.70 (0.593) | 15.53 (2.073) |
| 60.1 (4.07) | 10.0 (0.00) | 100.0 (5.56) | 0.80 (0.054) | 2.17 (0.149) | 17.67 (0.807) | 15.62 (2.455) |
| 60.0 (6.33) | 10.0 (0.00) | 98.9 (7.57) | 0.80 (0.054) | 2.15 (0.174) | 17.53 (1.142) | 15.24 (2.866) |
| 60.3 (8.33) | 10.0 (0.00) | 99.9 (9.31) | 0.80 (0.054) | 2.15 (0.198) | 17.48 (1.411) | 15.47 (3.341) |
| 59.0 (10.57) | 10.0 (0.00) | 99.0 (11.02) | 0.80 (0.047) | 2.15 (0.202) | 17.48 (1.773) | 15.55 (3.532) |
| 60.0 (0.00) | 10.0 (0.46) | 100.2 (2.92) | 0.80 (0.058) | 2.17 (0.121) | 17.73 (0.475) | 15.61 (1.612) |
| 60.0 (0.00) | 10.0 (1.04) | 100.1 (3.15) | 0.80 (0.0563) | 2.17 (0.122) | 17.72 (0.593) | 15.59 (2.073) |
| 60.0 (0.00) | 9.9 (1.51) | 100.2 (3.38) | 0.80 (0.067) | 2.17 (0.131) | 17.74 (0.807) | 15.58 (2.455) |
| 60.0 (0.00) | 10.0 (1.85) | 100.1 (3.57) | 0.80 (0.071) | 2.17 (0.139) | 17.72 (1.142) | 15.57 (2.866) |
| 60.0 (0.00) | 10.0 (2.45) | 100.3 (4.13) | 0.81 (0.082) | 2.17 (0.164) | 17.72 (1.411) | 15.62 (3.341) |
| 59.6 (5.79) | 10.1 (1.40) | 99.9 (8.48) | 0.81 (0.067) | 2.17 (0.213) | 17.65 (1.293) | 15.66 (3.066) |
| 58.5 (9.68) | 10.4 (2.46) | 98.5 (12.25) | 0.80 (0.065) | 2.15 (0.266) | 17.36 (1.971) | 15.21 (3.881) |

[a,b] Simulated values for [a]$\mu BW_0$ and ($\sigma BW_0$) and [b]$\mu$EX and ($\sigma$EX) respectively. [c]Result of variation in growth potential only.

### *5.4.2. Comparison of the average pig and mean population response*

*5.4.2.1. Group Size.* There were no differences in the predicted response of the average pig and the mean population response for any of the performance parameters. Mean performance was predicted to decrease as N increased. Variation in performance of the mean population was predicted to increase with increasing N. An increase in $\sigma t$ from 2.9 to 4.6 days was predicted to occur as N was increased from one to 100 (results not shown).

*5.4.2.2. Space Allowance.* As A was decreased the ADG and ADFI of both the average pig and the population decreased once the value of SPA fell below a critical value ($SPA_{crit}$ $m^2/BW^{0.67}$). The population response was predicted to differ from the response of the average pig, with a curvilinear, as opposed to a linear-plateau,

response (Figure 5.1). A value of 0.66 $m^2$/pig was predicted for the $SPA_{crit}$ of the mean population compared to 0.62 $m^2$/pig for the average pig. A decrease in the variation of the mean population response was found as SPA was decreased.

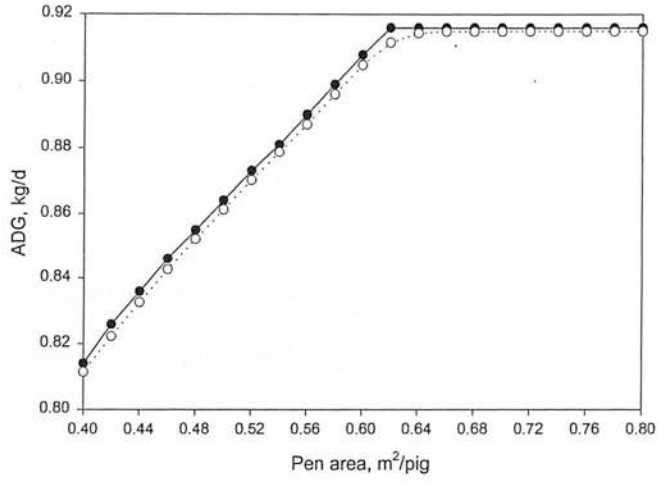


**Figure 5.1.** *Predicted effect of space allowance on the average daily gain (ADG) response of the average individual (●) and the mean population (○) of 60 kg pigs.*

*5.4.2.3. Mixing.* No differences were found in the responses to mixing of the average pig and the mean population. In both cases, mixing increased t from 53 to 58 days, and decreased both ADG and ADFI from 0.76 to 0.69 kg/d and from 2.10 to 1.98 kg/d respectively. Figure 5.2 shows the time course of the effect of mixing on ADG for two particular individuals chosen from the population. Pig A was predicted to show a 6 % decrease in ADG and take an extra three days to reach $BW_f$ due to mixing. Pig B was predicted to show a 12 % decrease in ADG and require an extra 10 days to reach $BW_f$.

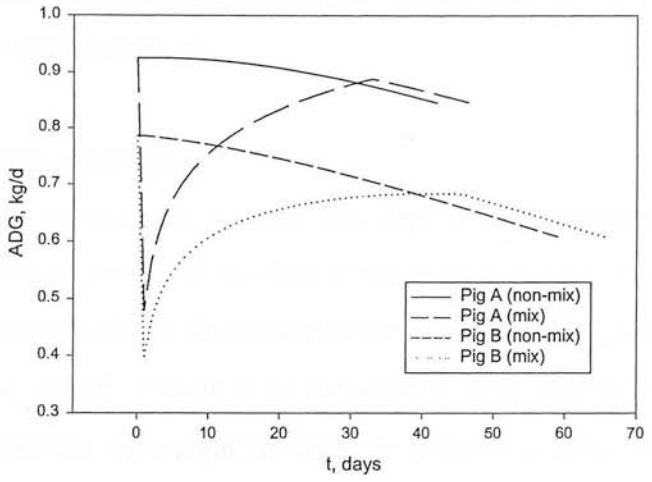


***Figure 5.2.*** *Time course (t) effect of mixing on the average daily gain (ADG) of two randomly chosen individuals from the population. Mixing either occurred or not on day one and the simulation period was from an initial mean BW of 60 kg to a final BW of 100 kg.*

*5.4.2.4. Temperature.* As temperature increased the ADG and ADFI of both the average pig and the population decreased once the value of temperature reached the upper critical temperature ($T_u$, °C). A linear-plateau response was predicted for the average pig and a curvilinear-plateau response for the population response. Values of 26 and 28 °C were predicted for the $T_u$ of the average pig and mean population respectively. A decrease in the variation of the mean population response was predicted as temperature increased (results not shown).

## 5.5. Discussion

Proper allowance for population variation is important when models are used to predict nutrient requirements (Fisher *et al*, 1973; Curnow, 1973, 1986), optimise pig production systems (Pomar *et al.*, 2003) and devise animal breeding strategies (Knap, 1995). Knowledge of between animal variation is important in commercial situations, especially for all-in-all-out systems as variation in carcass weight and composition i.e., the homogeneity of a group, will partly determine enterprise profitability. The aim here was to demonstrate the impact on pig performance of

individual variation in potential growth and initial state and in the ability to cope when exposed to social stressors.

### 5.5.1. Variation in initial state

One of the main factors determining the degree of homogeneity of a group at slaughter is the homogeneity at the start of the growth period. Variation in $BW_0$ was predicted to increase both the time taken to reach a given $BW_f$ and the $BW_f$ achieved over a given time period. If there is no variation in $BW_0$ ($\sigma BW_0 = 0$) all pigs need to gain the same amount of weight in order to achieve a given $BW_f$. As $\sigma BW_0$ is increased, the BW gain needed to achieve $BW_f$ varies due to simulated differences in $BW_0$. Similarly, over a specified number of days individuals with greater $BW_0$'s are generally able to achieve a superior $BW_f$ than counterparts with lower $BW_0$'s.

Predicted variation in body composition was affected by increasing $\sigma BW_0$ only in the 'set time' simulations. This is because increasing variation in $BW_0$ necessarily leads to increased variation in $BW_f$ over a set number of days, which in turn leads to greater variance in P and L weights. The point can be illustrated by an example. At the end of the simulation period, one individual was predicted to have a $BW_f$ of 105 kg with 18.5 and 15.9 kg of P and L respectively. Another was predicted to have a $BW_f$ of 98 kg, with 17.3 and 15.4 kg of P and L respectively. Variation in $BW_0$ was predicted to affect the variation in the growth response to substantial extent. Improving management techniques to decrease variation in $BW_0$ is therefore likely to increase the homogeneity of a group at slaughter.

### 5.5.2. Variation in ability to cope

It has been shown in a number of studies that pigs classified as dominant tend to outperform their subordinates. This has been demonstrated when pigs are grouped (McBride *et al.*, 1964; Hansen *et al.*, 1982), mixed (Hessing *et al.*, 1994; D'Eath, 2002) and when FSA is limiting (Giroux *et al.*, 2000). There is also evidence that social dominance is positively correlated to BW in pigs (Brouns and Edwards, 1994; Erhard and Mendl, 1997; Drickamer *et al.*, 1999; D'Eath, 2002). Taken together these results suggest that larger pigs within a group tend to be dominant and to cope

better when conditions are sub-optimal, i.e., when pigs are exposed to stressors. It was assumed in the model that there is a negative correlation between $BW_0$ and EX.

Variation in EX was generated as a first step towards accounting for behavioural differences between individuals of a population and quantifying the resulting effects on population performance. This has not been achieved in previous stochastic modelling attempts e.g., Knap (2000a) and Pomar *et al.* (2003), where the effects of social stressors and any differences in ability to cope are absent. It was predicted that variation in the growth response of a population was increased by the inclusion of variation in EX when pigs were housed in conditions likely to be encountered in commercial environments. Any improvement in the pigs' ability to cope would allow a greater proportion of their potential to be attained under stressful conditions and may be a better way of improving pig performance and enterprise profitability than increasing potential *per se*. If increased growth rate and ability to cope are antagonistic as suggested by Grandin and Deesing (1998), then trying to increase pig performance achieved under excellent conditions, i.e., improving potential alone, may not prove to be the best selection strategy.

There is literature suggesting that the ability to cope is negatively correlated with rapid growth rate and lean content. Schinckel *et al.* (2003) noted that 'pigs from populations with above average percent carcass lean have a greater percentage reduction in live weight and carcass lean growth than pigs of average percent carcass lean' when exposed to stressors. Torrey *et al.* (2001) reported a genetic relationship between loin eye area and the ability to adjust to mixing with unfamiliar pigs. Grandin (1994) noted that 'the appearance of highly excitable and difficult to handle animals appeared to coincide with the genetic selection for both rapid growth and high, lean meat yield'. If EX and lean growth rate are adversely correlated there may be negative implications regarding the welfare of pigs selected for lean growth. Selection for improved lean growth rate would then indirectly lead to selection for poorer ability to cope in the population. Since EX depends in part upon the structure of the group, then group selection may be necessary in order to improve the ability of animals to cope when exposed to social stressors. The experiments of Muir and

Schinckel (2002) with quail and Muir (1996) and Muir and Craig (1998) with poultry, demonstrate that selection for desirable associate effects within a group may be a means to select animals which are better adapted to their rearing environment. Any genetic correlation between EX and the growth parameters that can be evaluated could be included in the model by incorporating the co-variation between the identified parameters and EX.

The effect of varying values of EX was discussed in Chapter four. The apparent quantitative effects of different amounts of variation in EX, i.e., the value of $\sigma$EX, follows from the scaling used. This was set so that a unit change in EX produced deviations of approximately one percent from the mean performance. However, it may be that the scaling made is inappropriate and that the model is too insensitive to between animal variation in EX. More information is needed to quantify the variation of EX within a population and its effects on performance.

### *5.5.3. Individual and mean population responses*

Ferguson *et al.* (1997) stated that 'there is a marked difference in the response of the average individual in the population and the mean population response'. Pomar *et al.* (2003) demonstrated that there are clear differences between the predicted average individual and the mean population response for the rate of protein retention in response to increasing dietary protein intake. However, differences between the average pig and mean population responses should not always be expected, and it will depend partly upon the stressors to which the pigs are exposed. Where all individuals become adversely affected at the same stressor intensity, e.g., being housed individually as opposed to being in a group or being mixed or not, then no differences between the average individual and mean population response is to be expected. This is because all individuals are either affected or not, although this may be to varying extents. If however the intensity at which the stressor becomes limiting is able to differ between individuals, e.g., $SPA_{crit}$, critical FSA and UCT, differences between the average individual and mean population response are expected.

The linear-plateau response of the average individual to decreasing SPA is a direct outcome of the assumption used in the model (see Chapter four for further details). The curvilinear-plateau response of the population however can be explained by individual differences in $SPA_{crit}$, generated from between-animal variation in BW and EX (Figure 5.1). The plateau is predicted to occur when $SPA > SPA_{crit}$ for all pigs in the population and the curvilinear transition phase occurs when only a proportion of the population is constrained, i.e., $SPA < SPA_{crit}$ for only some individuals. As the intensity of the stressor increases the proportion of the population that is constrained increases until all individuals are affected. At a fixed SPA the proportion of pigs limited will increase with increasing population variance and this will result in a greater degree of curvature. This was demonstrated by Pomar *et al.* (2003) for average daily rate of protein retention in response to increasing protein intake. The mean population and individual responses to decreasing SPA are predicted to differ over only a small range of pen area. However, this quantitative finding may underestimate the position in commercial enterprises and could have important financial consequences when space is at a premium.

The type of stressor also influences the amount of variation in the mean population response to increasing stressor intensity. If the critical limit does not vary between individuals, then an increase in variation is expected as the intensity of the stressor increases. This is a direct result of individual differences in ability to cope with the stressor. Conversely, a decrease in variation is expected if the critical limit is able to vary between individuals. This is because some individuals will be limited at lower stressor intensity than others and consequently a narrower range of variation is expected as the intensity of the stressor increases. For example, the increased range of $ADG_p$ and $FI_d$ of individuals with increased potential will not be expressed at high temperatures and low SPA's because of thermal and space constraints respectively. Individuals with a lower potential will be less affected at a given temperature and space allowance, as they will have a lower critical space allowance and higher UCT. Consequently, a narrower range of ADFI and ADG is predicted as SPA decreases and temperature increases.

Individual differences in ability to cope in differing thermal environments are not made explicit in the model. However, because of individual variation in BW, potential rates of gain, fatness and levels of activity, between animal variation in ability to cope with the thermal environment is simulated. These differences directly influence the individuals upper and lower critical temperature ($T_l$, °C) and enable some individuals to cope better in a given thermal environment than others. For example, smaller, slower growing, thinner and less active individuals will be better able to cope at high temperatures and less able to cope at low temperatures than larger, faster growing, fatter, and more active individuals. This is a consequence of lower $T_u$'s and higher $T_l$'s respectively.

### *5.5.4. Future developments*

The introduction of variation in EX and $BW_0$ into the model is likely to allow better estimates of the phenotypic variation in pig performance observed in experiments with real pigs to be derived. A comparison between model predictions and experimental data is a necessary next step. The pig's response to encountered stressors may be as important as the pig's genetic potential for growth when pigs are reared in commercial conditions. Methods to characterise mean values of B*, $P_m$ and $L_m/P_m$ have been suggested by Ferguson and Gous (1993) and Knap *et al.* (2002) and variances estimated by Ferguson *et al.* (1997) and Knap (2000a). A measure of $\mu$EX and $\sigma$EX for specific populations is still required. Quantifying the variation in EX may improve the rate of breeding for improved ability to cope, as the amount of variation determines the degree of selection pressure able to be applied. Comparing the variation predicted by the model with experimental variation will allow an initial estimate of the variation in EX to be made. This was the method used by Ferguson *et al.* (1997) when predicting the variation in B*, $L_m/P_m$ and $P_m$ from variability in ADG and ADFI and external estimates of the heritabilities of the traits. If the simplistic assumption that individuals react in the same way to all types of social stressors is incorrect, then the introduction of further parameters, in addition to EX, may be required for a sufficient descriptor of ability to cope when exposed to social stressors.

# Chapter 6

## Variation in the performance of growing pigs: comparing experimental observations with model predictions

## 6.1. Abstract

Stochastic models are able to predict the amount of variability as well as the mean population response. This is essential in understanding the biological mechanisms implicated in the response of populations to treatments, predicting nutrient requirements, comparing and optimising production systems and for animal breeding purposes. The objective here was to compare the level of variation observed in the performance of growing pigs with that predicted by a population model to determine to what extent variation in potential growth, initial state ($BW_0$) and ability to cope when exposed to social stressors (EX), influence the variation generated. A secondary aim was to quantify the inevitable error of measurement and investigate the effect this may have on model predictions. Comparisons were made between the phenotypic and genetic variation ($CV_g$) observed in pigs under experimental conditions with that determined by the model. Three models were simulated: model one included variation in growth potential only, model two included variation in $BW_0$ in addition to variation in growth potential and model three included variation in growth potential, $BW_0$ and EX. In all cases all three models generated less variation than the phenotypic variation observed. The inclusion of variation in $BW_0$ and EX into the model increased the amount of variation predicted in all cases. Variation in the growth parameters accounted for the majority of the generated variation (45 to 83 %), followed by variation in $BW_0$ (4 to 46 %) and variation in EX (1 to 14%). All three models simulated levels of variation within or above the estimated range of $CV_g$. It is likely that the model underestimated the phenotypic variation observed in real experiments for a number of reasons. These include measurement errors that cause the true phenotypic variation to be overestimated, missing information about the treatment groups used in the experiments, which preventing the model from being fully calibrated, and the lack of an accurate estimate of the variation in EX within a population. The extent of measurement errors, caused by factors such as differential gut fill, balance reading errors and food spillage, was estimated to be approximately one percent. This may be of importance when interpreting and evaluating model predictions, especially when predictions are over a short period of time or small weight range.

## 6.2. Introduction

Variation between individuals is often ignored when decisions are made with reference to populations (Curnow, 1986), and results in the literature are mainly interpreted as average responses to treatments with little emphasis given to the variation around the means. There are however, many good reasons to consider between animal variation. The efficiency of a production system for example is determined by the efficiency of individual animals and profitability may be affected to a large extent by the amount of variation in production traits (Knap, 1995). The degree of variation around the mean population response can help in understanding the biological mechanisms implicated in the response of populations to treatments (Pomar *et al.*, 2003), predicting nutrient requirements (Fisher *et al.*, 1973; Curnow, 1986), comparing and optimising production systems and for animal breeding purposes (Knap, 1995).

Stochastic models seek to predict the amount of variability as well as the mean population response and 'an accurate prediction of variability is a strong indication that the model is a good one' (Curnow, 1986). Therefore it is important that the predictions of models are compared with 'real' data obtained from experiments in order to determine the appropriateness and value of a model. The variation observed in real experiments comprises both genetic and environmental variation and so for meaningful comparisons with real data to be made, it is necessary to account for both components of variation when making model predictions. Stochastic pig growth models to date deal with genetic variation in growth potential only (Ferguson *et al.*, 1997; Knap 2000a and Pomar *et al.*, 2003). The exception is the population model described in Chapter five that deals with variation in initial state and ability to cope when exposed to social stressors (EX). Initial state, described by initial BW ($BW_0$, kg) and body composition, depends largely on the potential of the individual. However, non-genetic components of the environment will also influence the animal variation in $BW_0$ between of a group. Even under the best experimental conditions there is likely to be variation in initial state between animals at the start of the trial period. Variation in EX is likely to exists between individuals and is determined by the genotype of the individual and the social environment to which it is exposed.

Including variation in $BW_0$ and EX into a population model is a first step at accounting for some of the variation in non-genetic components that may influence the performance of populations.

The starting point of this study was the population model described in Chapter five that predicts the effects of the social, physical and nutritional environments on pig performance. The objective was to compare the level of phenotypic variation observed in the performance of growing pigs with that predicted by the model to determine to what extent variation in potential growth, $BW_0$ and EX influence the variation generated. A secondary aim was to quantify the inevitable error of measurement and investigate the effect this may have on model predictions.

## 6.3. Materials and methods

### *6.3.1. Data*

Two experiments conducted at the Meat and Livestock Commission (MLC) facilities were identified to give a measure of the phenotypic variation observed in real pigs under experimental conditions. These experiments were chosen as they provided repeated body weight measures on individuals over a wide weight range and information on daily feed intake. Individuals were categorised into treatment groups for the data analysis in order to determine the variation between individuals treated alike. Details on experimental treatments were not provided as these were covered by a confidentiality agreement.

*6.3.1.1. Data set one.* Data on pig performance from 25 to 100 kg were from a 5 x 2 x 6 factorial arrangement (n = 651) experiment with five genotypes of two sexes on six treatments. Actual weights at nominal weights of 30, 50, 70 and 90 kg were recorded in addition to $BW_0$ and slaughter weight ($BW_f$, kg). Animals were housed in pairs and daily feed intake was recorded per pen. It was assumed that both individuals in the pen consumed equal amounts. Only 55 of the expected 60 treatment groups were available, as no treatment three by sex two treatment groups were present. The data from 33 individuals were removed, as they were incomplete. One animal was removed due to an extremely slow rate of gain. This resulted in a

mean treatment group size of 11.2 for estimates of average daily gain (ADG, kg/day), average daily feed intake (ADFI, kg/d) and feed conversion efficiency (FCR, kg feed / kg gain).

*6.3.1.2. Data set two.* Data on pig performance from 45 to 95 kg came from a 2 x 2 x 3 x 2 x 2 factorial arrangement (n = 916) experiment with two genotypes of two sexes, three treatments, two feeds and two group sizes (2 and 5 pigs/pen). In addition to $BW_0$ and $BW_f$, feed intake per pen was recorded on a daily basis. Of the possible 48 treatment groups, only 21 were present mainly due to the absence of genotype two by group size two treatment groups. Data from ten individuals were removed, as they were incomplete. This gave an average of 43 pigs/treatment. Feed intake was recorded in only 13 of the 21 treatment groups.

*6.3.1.3. Data analysis.* Mean values and the variation within the treatment groups were estimated assuming that the data were normally distributed. Values for ADG, ADFI and FCR were calculated for each of the treatment groups in both data sets. In data set one ADG, ADFI and FCR values were calculated between the BW ranges 30 to 50, 50 to 70, 70 to 90 and 30 to 90 kg. In data set two, calculations were made over the BW range 45 to 95 kg only. The means and standard deviations (STD) for each of the treatment groups were averaged to give an overall mean, STD and coefficient of variation (CV) for ADG, ADFI and FCR. The Bartlett test was performed in the statistical package Minitab (Minitab Incorporated, 1998) to test for the homogeneity of variance between treatment groups.

The heritability ($h^2$) of a trait is an estimate of the genetic proportion of the phenotypic variation. Multiplying the calculated CV's of ADG and ADFI by the square root of respective heritabilities allows estimates of the genetic variation ($CV_g$) of ADG and ADFI to be made. To accommodate a range of published heritabilities (e.g., Stewart and Schinckel, 1989; van Steenbergen *et al.*, 1990; Mrode and Kennedy, 1993; Cameron and Curran, 1994) the $CV_g$ values were calculated using $h^2$ values of 0.15 and 0.50 for ADG and 0.20 and 0.60 for ADFI. An average $CV_g$ using a $h^2$ value of 0.30 for both ADG and ADFI was also calculated.

### 6.3.2. Model

The theory behind the population model outlined in Chapter five is briefly described. The model uses four genetic descriptors to characterise the pig genotype: protein weight at maturity ($P_m$, kg), the ratio of lipid to protein at maturity ($L_m/P_m$, kg/kg), a scaled rate parameter (B*, kg/day/$kg^{0.73}$) and the ability to cope when socially stressed (EX). The initial state of the pig is described by initial body weight ($BW_0$, kg) from which the chemical composition of the pig is calculated assuming the pig has its ideal body composition determined by its genotype. The potential rate of protein gain is determined by pig genotype and current protein content only. The potential gains of the other chemical components are determined from potential protein gain assuming allometry between the components (Emmans, 1988; Emmans and Kyriazakis, 1997). Potential daily gain ($ADG_p$, kg/d) is the sum of the potential gains of the chemical components; gut fill is assumed to be five percent of the gain (Moughan *et al.*, 1987).

Desired feed intake is predicted in the model as the amount of feed required that will satisfy their energy and protein requirements for $ADG_p$, maintenance and any compensatory lipid gain as described in Chapter two. Actual intake is subject to capacity constraints of the animal to consume feed bulk, its ability to maintain thermoneutrality and consequences of the social environment. The physical environment determines whether the pig is hot, cold or thermoneutral and is described in detail in Chapter two. Factors in the social environment, i.e., group size (N), space allowance (SPA, $m^2/BW^{0.67}$), feeder space allowance (FSA, feeder spaces/pig), and the occurrence of mixing, may act as stressors and decrease performance by lowering pigs ability to attain their potential. The exception is FSA that directly constrains intake when limiting. The descriptor, EX, adjusts both the intensity of the stressor at which the pig becomes stressed and the extent to which each stressor reduces performance at a given stressor intensity. Increasing the value of EX represents increased sensitivity and a decreasing ability to cope when stressed. For further details of the social environment and how it affects pig performance see Chapter four.

For each simulated pig within a population, individual values for B*, $P_m$ and $L_m/P_m$ are generated independently at random from a normally distributed population using the estimated means and coefficients of variation to ensure that no correlation exists between the descriptors. Individual values for $BW_0$ and EX are then generated from their respective means and standard deviations (model inputs) whilst taking into account the generated genetic parameter values of the individual. It is assumed that individuals with the greatest potential will tend to have the highest $BW_0$ as would be expected from non-limiting growth. It is also assumed that there is a negative correlation between $BW_0$ and EX, i.e., bigger pigs are better able to cope when socially stressed (Brouns and Edwards, 1994; Drickamer *et al.,* 1999). Residuals are drawn at random and added to $BW_0$ and EX to represent non-genetic components such as the physical, social and nutritional environments which may cause the simulated phenotype to deviate from the genotype's potential. The values that characterise each animal are drawn before each simulation run and are able to be maintained for multiple simulation runs.

### *6.3.3. Simulation runs*

A total of 500 individuals were randomly generated in order to compare the variation predicted by the model with the average within treatment group variation observed in the experimental data sets. From the genetic lines parameterised in the literature, the one found to give the closest fit to the average treatment group performance calculated for each data set was used. The estimated mean parameter values and CV's were kept constant throughout model simulations. The mean population response and variation of the model outputs were determined from the individual pig responses.

The feed was kept the same in all simulations. It contained 14.2 MJ digestible energy and 180 g crude protein (CP) per kg food. The biological value used to describe the quality of the protein was fixed at 0.89 and CP digestibility at 0.83 kg/kg. Water holding capacity, a measure of feed bulk (Kyriazakis and Emmans, 1995), was fixed at 3 kg/kg. The physical environment was ambient temperature = 20 °C, air velocity = 0.15m/s, relative humidity = 40 % and floor thermal resistance = 0.07 $°C.m^2$ to

represent concrete slats. The social environment was fixed at a SPA of one $m^2$/pig, one feeder space per ten pigs, no mixing and N represented that reported in each of the data sets. A value of two was used for data set one and a value of 3.5 in data set two to represent the mean group size.

Three models were simulated for each data set to investigate the impact of including between animal variation in growth potential, $BW_0$ and EX on the variation in performance generated by the model. Model one included variation in growth potential only, i.e., the genetic parameters B*, $L_m/P_m$ and $P_m$. Model two included variation in $BW_0$ in addition to variation in growth potential and model three included variation in growth potential, $BW_0$ and EX. The mean and standard deviation of $BW_0$ used in the model simulations (models two and three) were the values observed in the experimental data sets. A value of ten was used for the mean value of EX in all three models and a value of two was assigned to the standard deviation of EX in model three. Where no variation was generated in $BW_0$ (model one) and EX (model one and two) the standard deviations of the parameters were fixed at zero.

### *6.3.4. Measurement errors*

The sequential daily BW data of growing pigs collected by Kyriazakis (1989) were used to make an estimate of the minimum error of measurement. Daily BW measurements of 31 individuals from approximately 20 to 30 kg were analysed. The mean residual standard deviation (rsd, kg) of the BW versus time regressions of the individual pigs were calculated and averaged to give an overall mean estimate for rsd. This is taken to be the mean error of measurement.

The model was run from $BW_0 \pm$ rsd to $BW_f \pm$ rsd to assess its impact on performance predictions. Two BW ranges were used. In both cases $BW_0 = 30 \pm$ rsd kg and $BW_f$ was set at 50 ± rsd and 90 ± rsd kg in weight range one and two respectively to represent a typical grower and grower/finisher system. It was assumed that there was no error in the time between measurements, i.e., pigs were weighed on exact daily intervals.

## 6.4. Results

### *6.4.1. Data analysis*

Average treatment group means for data sets one and two are shown in Tables 1 and 2 respectively, along with their corresponding STD's and CV's. The average treatment group STD and CV represent within group variation. Between treatment group STD's, i.e., between group variation, are also shown (in brackets).

**Table 1.** *Mean values and the variation within treatment groups for data set [a]one. Standard deviations of the treatment group mean and standard deviations, i.e., between treatment group variation are shown in brackets. ADG, ADFI and FCR are the average daily gain, average daily feed intake and feed conversion efficiency respectively*

| [b]Trait | Treatment group mean | Treatment group standard deviation | Treatment group coefficient of variation | [c]Bartlett test |
|---|---|---|---|---|
| $BW_{30}$, kg | 30.93 (0.849) | 3.353 (0.8318) | 0.108 | *** |
| $BW_{50}$, kg | 51.03 (0.686) | 4.850 (1.3314) | 0.095 | *** |
| $BW_{70}$, kg | 71.69 (1.051) | 6.375 (1.9626) | 0.089 | *** |
| $BW_{90}$, kg | 85.75 (2.557) | 8.123 (2.4871) | 0.095 | *** |
| $ADG_{30-50}$, kg/d | 0.75 (0.074) | 0.172 (0.0581) | 0.234 | *** |
| $ADG_{50-70}$, kg/d | 0.82 (0.074) | 0.184 (0.0644) | 0.228 | *** |
| $ADG_{70-90}$, kg/d | 0.81 (0.086) | 0.226 (0.0925) | 0.284 | *** |
| $ADG_{30-90}$, kg/d | 0.76 (0.048) | 0.113 (0.0347) | 0.149 | *** |
| $ADFI_{30-50}$, kg/d | 1.61 (0.113) | 0.219 (0.0944) | 0.136 | * |
| $ADFI_{50-70}$, kg/d | 2.03 (0.137) | 0.283 (0.1129) | 0.139 | NS |
| $ADFI_{70-90}$, kg/d | 2.36 (0.182) | 0.400 (0.2003) | 0.168 | ** |
| $ADFI_{30-90}$, kg/d | 1.92 (0.106) | 0.207 (0.0721) | 0.108 | NS |
| $FCR_{30-50}$, kg/kg | 2.21 (0.214) | 0.328 (0.1358) | 0.149 | * |
| $FCR_{50-70}$, kg/kg | 2.59 (0.208) | 0.433 (0.1815) | 0.167 | NS |
| $FCR_{70-90}$, kg/kg | 3.04 (0.297) | 0.626 (0.3360) | 0.203 | *** |
| $FCR_{30-90}$, kg/kg | 2.54 (0.157) | 0.236 (0.0943) | 0.093 | NS |

[a]Total of 617 animals in 55 different treatment groups

[b]Subscripts represent the weight range

[c]The Bartlett test tests for homogeneity of variance between treatment groups

**Table 2.** *Mean values and the variation within treatment groups for data set [a]two. Standard deviations of the treatment group mean and standard deviations, i.e., between treatment group variation are shown in brackets ADG, ADFI and FCR are the average daily gain, average daily feed intake and feed conversion efficiency respectively*

| [b]Trait | Treatment group mean | Treatment group standard deviation | Treatment group coefficient of variation | [c]Bartlett test |
|---|---|---|---|---|
| $BW_{45}$, kg | 45.6 (1.250) | 4.188 (0.5549) | 0.093 | NS |
| $BW_{95}$, kg | 94.9 (3.921) | 10.20 (1.6286) | 0.107 | * |
| $ADG_{45\text{-}95}$, kg/d | 0.75 (0.088) | 0.117 (0.0161) | 0.156 | NS |
| $ADFI_{45\text{-}95}$, kg/d | 1.93 (0.293) | 0.176 (0.0888) | 0.083 | *** |
| $FCR_{45\text{-}95}$, kg/kg | 2.57 (0.160) | 0.245 (0.0814) | 0.088 | *** |

[a]Total of 906 pigs in total of 21 different groups

[b]Subscripts represent the weight range

[c]The Bartlett test tests for homogeneity of variance between treatment groups

Within treatment group mean values, STD's and CV's for ADG, ADFI and FCR were comparable between data sets one and two, over the full BW range investigated, i.e., 30 to 90 kg and 45 to 95kg in data sets one and two respectively. The CV for the BW measurements within groups is consistent in both data sets at around 0.10 in all cases. In data set one the mean treatment group variation in ADG, ADFI and FCR is larger in the three shorter weight periods, especially the 70 to 90 kg range, than the longer 30 to 90 kg period.

The amount of variation between treatment groups tended to be larger in data set two. For example the between treatment variation in mean $ADG_{30\text{-}90}$ and $ADFI_{30\text{-}90}$ in data set one were 0.048 and 0.106 kg/d respectively compared to $ADG_{45\text{-}90}$ and $ADFI_{45\text{-}90}$ values 0.088 and 0.293 kg/d respectively in data set two. The Bartlett test demonstrated significant differences in the homogeneity of variation between treatment groups in the majority of the performance parameters.

### *6.4.2. Simulation results*

The genetic lines characterised by Knap (2000a) ($B^*$ = 0.0323 (0.03), $P_m$ = 32.5 (0.07) $L_m/P_m$ = 3.2 (0.10)) and Ferguson *et al.* (1997) ($B^*$ = 0.0294 (0.02), $P_m$ = 38.0

(0.10), $L_m/P_m$ = 2.5 (0.15)) were found to give ADG values closest to data sets one and two respectively. Values for the two genotypes were used in all model simulations and the between animal variation in the genetic parameters, coefficients of variation shown in brackets, were maintained throughout.

**Table 3.** *The effect of including variation in potential growth (model 1), initial BW (model 2) and ability to cope when exposed to social stressors (model 3) on the simulated coefficient of variation of average daily gain (ADG) and average daily feed intake (ADFI) and a comparison with the phenotypic and genetic variation ($CV_g$) observed from the data sets*

| [a]Trait | Observed CV | [b,c]$CV_g$ | [d] Model 1 | [e] Model 2 | [f] Model 3 |
|---|---|---|---|---|---|
| [g]Data set one | | | | | |
| $ADG_{30-50}$, kg/d | 0.234 | 0.0906 - 0.1655 (0.1282) | 0.0381 | 0.0572 | 0.0623 |
| $ADG_{50-70}$, kg/d | 0.228 | 0.0883 - 0.1612 (0.1249) | 0.0429 | 0.0590 | 0.0614 |
| $ADG_{70-90}$, kg/d | 0.284 | 0.1100 - 0.2008 (0.1556) | 0.0557 | 0.0653 | 0.0676 |
| $ADG_{30-90}$, kg/d | 0.149 | 0.0577 - 0.1054 (0.0816) | 0.0440 | 0.0617 | 0.0672 |
| $ADFI_{30-50}$, kg/d | 0.136 | 0.0608 - 0.1053 (0.0745) | 0.0372 | 0.0753 | 0.0835 |
| $ADFI_{50-70}$, kg/d | 0.139 | 0.0622 - 0.1077 (0.0761) | 0.0389 | 0.0717 | 0.0726 |
| $ADFI_{70-90}$, kg/d | 0.168 | 0.0751 - 0.1301 (0.0504) | 0.0454 | 0.0756 | 0.0778 |
| $ADFI_{30-90}$, kg/d | 0.108 | 0.0483 - 0.0837 (0.0592) | 0.0394 | 0.0699 | 0.0767 |
| [h]Data set two | | | | | |
| $ADG_{45-95}$, kg/d | 0.156 | 0.0604 – 0.1103 (0.0854) | 0.0602 | 0.0630 | 0.0729 |
| $ADFI_{45-95}$, kg/d | 0.083 | 0.0371 – 0.0643 (0.0455) | 0.0496 | 0.0672 | 0.0758 |

[a]Subscripts represent the weight range.

[b]The range of $CV_g$ for ADG is calculated by multiplying the published phenotypic variation by $\sqrt{0.15}$ and $\sqrt{0.50}$ $h^2$ values. The figure in brackets is the estimate using the average $h^2$ value of $\sqrt{0.30}$.

[c]The range of $CV_g$ for ADFI is calculated by multiplying the published phenotypic variation by $\sqrt{0.20}$ and $\sqrt{0.60}$ $h^2$ values. The figure in brackets is the estimate using the average $h^2$ value of $\sqrt{0.30}$.

[d]Model 1 = variation in potential growth only.

[e]Model 2 = variation in potential growth and initial body weight.

[f]Model 3 = variation in potential growth, initial body weight and ability to cope when exposed to social stressors.

[g]Total of 617 animals in 55 different treatment groups

[h]Total of 906 pigs in total of 21 different groups

Table 3 shows the variation predicted by the three models in comparison to the treatment group mean variation observed in each of the data sets. The range of $CV_g$'s estimated from the observed phenotypic variation and published estimates of $h^2$ for ADG and ADFI is also shown. The inclusion of variation in $BW_0$ and EX into the model increased the amount of variation predicted in all cases as expected. The percentage of the total variation generated by model simulations accounted for by variation in the genetic growth parameters (model one), initial BW (model two) and ability to cope when exposed to social stressors (model three) is shown in Table 4. Variation in the growth parameters accounted for the majority of the generated variation (45 to 83 %), followed by variation in $BW_0$ (4 to 46 %) and variation in EX (1 to 14%).

**Table 4.** *Percentage of total variation generated by model simulations accounted for by variation in the genetic growth parameters (Potential), initial BW ($BW_0$) and ability to cope when exposed to social stressors (EX). ADG and ADFI are the average daily gain and average daily feed intake respectively*

| [a]Trait | Potential | $BW_0$ | EX |
|---|---|---|---|
| [b]Data set one | | | |
| $ADG_{30-50}$, kg/d | 61.2 | 30.7 | 8.2 |
| $ADG_{50-70}$, kg/d | 69.9 | 26.2 | 3.9 |
| $ADG_{70-90}$, kg/d | 82.4 | 14.2 | 3.4 |
| $ADG_{30-90}$, kg/d | 65.5 | 26.3 | 8.2 |
| $ADFI_{30-50}$, kg/d | 44.6 | 45.6 | 9.8 |
| $ADFI_{50-70}$, kg/d | 53.6 | 45.2 | 1.2 |
| $ADFI_{70-90}$, kg/d | 58.4 | 38.8 | 2.8 |
| $ADFI_{30-90}$, kg/d | 51.4 | 39.8 | 8.9 |
| [c]Data set two | | | |
| $ADG_{45-95}$, kg/d | 82.6 | 3.8 | 13.6 |
| $ADFI_{45-95}$, kg/d | 65.4 | 23.2 | 11.3 |

[a]Subscripts represent the weight range

[b]Total of 617 animals in 55 different treatment groups

[c]Total of 906 pigs in total of 21 different groups

Model predictions of CV for ADG and ADFI were similar over all the weight ranges, but were closer to the observed variation over the larger weight ranges, i.e., $ADG_{30-90}$

and $ADFI_{30-90}$ in data set one and ADG and ADFI in data set two (Table 4.). In all cases all three models generated less variation that the phenotypic variation observed. For data set one, all three models generated levels of variation below the estimated range of $CV_g$ for ADG. The exception was model two and three predictions for $ADG_{30-90}$ which were within the estimated range. Model predictions for ADFI in data set one were much closer to the estimated range of $CV_g$, with the predictions of models two and three close to the mean estimated $CV_g$. All three models simulated levels of variation within the estimated range of $CV_g$ in data set two, with model three generating levels of variation close to the phenotypic variation observed for $ADFI_{45-95}$.

### *6.4.3. Measurement errors*

The mean values for $BW_0$ and $BW_f$ of the 31 individuals were 19.70 and 32.12 kg respectively and the corresponding standard deviations were 0.825 and 1.311 kg. The mean number of consecutive BW measurements (days) was 17.5 with a standard deviation of 3.33 days. A mean rsd from the linear regression of 0.271 kg was calculated with a STD of 0.099 kg. This corresponds to approximately one percent of the mean BW of 25.91 kg.

Table 5 shows that including the estimated rsd, i.e., a one-percent error, in both $BW_0$ and $BW_f$ resulted in a maximum difference of 2.05 and 2.74 days in the simulated time taken to reach a $BW_f$ of 50 and 90 ± rsd kg respectively from $BW_0$ = 30 ± rsd kg. The maximum difference in the predicted time taken to reach 50 kg (2.05 days) was greater than the mean variation in t predicted by the model of 0.90 days, whereas the difference in the predicted time taken to reach 90 kg (2.74 days) was similar to the predicted mean variation of 2.89 days. No changes in the means and variability of ADG, ADFI and FCR were predicted by the inclusion of ± rsd.

**Table 5.** *Model predictions when taking account of the error of measurement* [a]*(residual standard deviation (rsd)) on the predicted performance of growing pigs from an initial BW ($BW_0$) of 30 ± rsd kg to a final BW ($BW_f$) of 50 ± rsd and 90 ± rsd kg respectively. ADG, ADFI, FCR and t the average daily gain, average daily feed intake, feed conversion ratio and time taken to reach $BW_f$ from $BW_0$ respectively. Standard deviations are given in brackets*

| $BW_0$, kg | $BW_f$, kg | ADG, kg/d | ADFI, kg/d | FCR, kg/d | t, days |
|---|---|---|---|---|---|
| 29.7 | 49.5 | 0.78 (0.025) | 1.63 (0.046) | 2.08 (0.060) | 25.84 (0.845) |
| 29.7 | 50.0 | 0.79 (0.026) | 1.64 (0.042) | 2.09 (0.060) | 26.35 (0.889) |
| 29.7 | 50.5 | 0.79 (0.029) | 1.65 (0.048) | 2.09 (0.067) | 26.96 (0.998) |
| 30.0 | 49.5 | 0.79 (0.025) | 1.64 (0.044) | 2.09 (0.065) | 25.41 (0.846) |
| [b]30.0 | [b]50.0 | [b]0.79 (0.027) | [b]1.65 (0.045) | [b]2.09 (0.064) | [b]25.91 (0.895) |
| 30.0 | 50.5 | 0.79 (0.027) | 1.66 (0.048) | 2.09 (0.065) | 26.50 (0.944) |
| 30.3 | 49.5 | 0.79 (0.027) | 1.65 (0.045) | 2.09 (0.063) | 24.91 (0.857) |
| 30.3 | 50.0 | 0.79 (0.028) | 1.65 (0.047) | 2.09 (0.068) | 25.47 (0.942) |
| 30.3 | 50.5 | 0.79 (0.028) | 1.66 (0.047) | 2.10 (0.064) | 26.08 (0.944) |
| 29.7 | 89.1 | 0.91 (0.039) | 2.23 (0.086) | 2.45 (0.082) | 66.02 (2.851) |
| 29.7 | 90.0 | 0.91 (0.045) | 2.23 (0.089) | 2.46 (0.079) | 66.98 (3.001) |
| 29.7 | 90.9 | 0.91 (0.038) | 2.24 (0.085) | 2.47 (0.083) | 68.05 (2.842) |
| 30.0 | 89.1 | 0.91 (0.040) | 2.22 (0.083) | 2.46 (0.082) | 65.92 (2.915) |
| [b]30.0 | [b]90.0 | [b]0.91 (0.040) | [b]2.24 (0.088) | [b]2.46 (0.079) | [a]66.41 (2.894) |
| 30.0 | 90.9 | 0.91 (0.041) | 2.25 (0.087) | 2.47 (0.083) | 67.30 (3.039) |
| 30.3 | 89.1 | 0.91 (0.040) | 2.24 (0.082) | 2.46 (0.081) | 65.31 (2.868) |
| 30.3 | 90.0 | 0.91 (0.041) | 2.25 (0.090) | 2.47 (0.084) | 66.09 (2.956) |
| 30.3 | 90.9 | 0.92 (0.038) | 2.26 (0.086) | 2.47 (0.077) | 66.76 (2.738) |

[a]mean residual standard error estimated as approximately one percent of BW from the sequential daily body weight measurements made by Kyriazakis (1989) in growing pigs

[b]No measurement error

## 6.5. Discussion

Allowing for population variation is essential when models are to be used to predict population responses, predict nutrient requirements or to economically optimise pig production systems (Pomar *et al.*, 2003). Stochastic models that properly represent populations are therefore needed to predict the response of a population. The objective of this study was to compare the simulated variation generated by the

population model described in Chapter five with the genetic and phenotypic variability in ADG and ADFI observed from two large data sets. Three models were simulated to determine to what extent variation in the genetic growth parameters (B*, $L_m/P_m$, and $P_m$), $BW_0$ and EX influenced and contributed to the variation generated in ADG and ADFI. An attempt to quantify the inevitable error of measurement was also made and the effect that this may have on model predictions was investigated.

### *6.5.1. Data analysis*

Explicit details of the genotypes, feed composition, ambient temperature and social conditions used in the specific treatment groups of the two data sets were not available. This information would have enabled the model to be better calibrated and allowed for a better test of the model.

Mean values for ADG, ADFI and FCR are similar for both data sets suggesting that differences between the genotypes and treatment groups used were small. As BW increased, the mean within treatment group CV of BW remained constant at approximately 0.1 kg representing no change in variance. This is not surprising and is a result of the pigs being on trial for a given weight range rather than over a given time period. Any differences in CV will therefore represent errors of measurement and management. If pigs were on trial for a given time period as opposed to weight period, variation in BW would be expected to increase as BW increased due to the wide range of growth rates achieved on the different treatment groups.

The mean within group variation (i.e., treatment group STD and CV) in ADG, ADFI and FCR was not as consistent as variation in BW. Mean within group variation was greater in the smaller weight ranges in data set one, i.e., 30 to 50, 50 to 70 and 70 to 90 kg, than the larger 30 to 90 kg range. Some of this difference is likely to be a result of measurement errors of weighing pigs. The longer the interval between weighing the less of a problem this becomes. The variation between treatment group means (i.e., STD of treatment group mean) in ADG and ADFI was larger in data set two when the 30-90 kg weight range of data set one is compared to the 45-95 kg weight range of data set two. The STD of the treatment group mean $ADFI_{30\text{-}90}$ in data

set one was 0.106 kg/d compared to 0.293 kg/d for $ADFI_{45-95}$ in data set two. As data set two is over a shorter weight period, then some increase in variation would be expected due to errors in measurement. It is likely that the remainder of the difference in the STD's of the treatment groups between the two data sets can be accounted for by differences in the treatments applied.

The range of $CV_g$ estimates for ADG and ADFI for the 30 to 90 kg weight range in data set one were similar with those of data set two (45-95 kg) and comparable to others calculated from the literature. The range of $CV_g$'s calculated from the data of Standal and Vangen (1985), Cameron *et al.*, (1988) and Mrode and Kennedy (1993) were 0.039-0.069, 0.044-0.078 and 0.041-0.076 respectively for ADG and 0.042-0.075, 0.056-0.085 and 0.049-0.086 respectively for ADFI. These compare with the values of 0.057-0.200 and 0.048-0.130 for ADG and 0.060-0.110 and 0.037-0.064 for ADFI in data sets one and two respectively. The reasonable agreement with the values published in the literature suggests that the levels of phenotypic variation observed in both data sets are sensible.

### *6.5.2. Simulation results*

Variation in the genetic growth parameters generates the majority of the variation in ADG and ADFI generated by the model simulations. The CV's used for B*, $L_m/P_m$ and $P_m$ for data sets one and two were estimates made by Knap (2000a) and Ferguson *et al.* (1997) respectively. As both sets of CV estimates are very similar for widely differing genotypes it is thought that they are likely to represent reasonable estimates for the range of genotypes used here. Including the variation in $BW_0$ observed in the data sets into the model (model two) increased the amount of variation generated in ADG and ADFI by as much as 51 % ($ADFI_{30-50}$ data set one). An increase in the variation of $BW_0$ would be expected to increase the generated variation in ADG and ADFI further (see Chapter five).

As EX is a conceptual variable no data are available from which the mean value and distribution of EX can be estimated for a population of pigs of a given genotype (breed). It is likely to require a large number of widely different populations reared in

a large number of differing conditions to determine experimentally the mean value and variation in EX along with possible correlation's with the growth parameters ($B^*$, $L_m/P_m$ and $P_m$). The mean value of EX was therefore assumed to be representative of the mean type of pig, EX = 10, and the standard deviation was fixed at two when included in the model, i.e., model three.

The variation generated by the inclusion of variation in EX into the model was small, accounting for between only 1 to 14 % of the total variation generated in ADG and ADFI. It was not reported to what extent the pigs were socially stressed and so consequently it was assumed in all model simulations that SPA and FSA were non-limiting and that pigs were not mixed. However, if the pigs were exposed to either limiting SPA or FSA or mixed, then the variation generated by the model would be expected to be greater. Furthermore, the standard deviation of EX used in model three was only estimated and may not have been accurate.

Levels of variation estimated by the three models were still much less than the phenotypic variation observed in the two data sets. However, the inclusion of variation in both $BW_0$ and EX increases the amount of variation generated and should be viewed as an improvement in model predictions. More accurate estimates of variation in EX and further details of the experimental conditions would almost certainly increase the variation predicted by the model. It is not likely that model predictions of variation will be as high as the phenotypic variation observed in real experiments. This is partly due to measurement errors that cause the true phenotypic variation to be overestimated.

### *6.5.3. Measurement error*

Data are subject to many sources of error. These include the effects of weighing errors (differential gut fill, balance reading errors and food spillage) and can be termed the inevitable error of measurement. Differences in time between recordings also causes errors when measuring rates, such as ADG and ADFI. If the time period between recordings is not equal then further inaccuracies will be introduced. The consequences of measurement errors may have significant impacts on the

interpretation of experimental results and on the prediction made by models. For example, Curnow (1986) demonstrated in an artificial example involving a population of spheres that increasing the coefficient of variation of the radius of an individual sphere from 5 to 50 % increased the percentage error in average surface area from 0.25 to 25.00 %.

It is thought that the error of measurement estimated from the sequential daily BW measures made by Kyriazakis (1989) of approximately one percent of the mean BW, is likely to represent the absolute minimum error. This is because in this experimental procedure great care was taken to weigh the animals on the same scales by the same person and at a consistent time of the day. A minimum error of approximately one percent BW equated to a maximum difference of 2.05 and 2.74 days of the predicted time taken to reach a $BW_f$ of 50 ± rsd and 90 ± rsd kg respectively and equates to 7.0 and 4.1 % respectively of the predicted mean time to reach $BW_f$. This highlights the care needed when interpreting model results as even a small error in measurement can have dramatic effects on model predictions. It may be especially important when interpreting predictions from an individual animal model, where no variation around the mean is predicted, and when predictions are for a short period of time or small weight range.

### *6.5.4. Conclusion*

A good global estimate of the variation of ADG and ADFI of growing pigs was obtained from two large-scale experiments containing a number of different genotypes and wide range of treatments. The inclusion of variation in $BW_0$ and EX into the model allowed better estimates of the variation observed in experimental conditions to be made and should be viewed as an improvement in model simulation. Variation in the growth parameters accounted for the majority of the generated variation, followed by variation in $BW_0$ and variation in EX. There are a number of reasons that the model underestimated the phenotypic variation observed in the experiments. These include measurement errors that cause the true phenotypic variation to be overestimated, missing information of the exact conditions applied in the treatment groups, which preventing the model from being fully calibrated, and

the lack of an accurate estimate of the variation present in EX within a population. As the evaluation process of a model involves not only the sole strict criteria of accuracy but also whether a given model is 'unusable' in answering specific questions (IPCC, 2001), this gives support to the value of the model in predicting the performance of populations of growing pigs.

# General Discussion

Simulation models allow the effects of multiple factors on animal performance to be considered simultaneously, including any interactions that may exist, in a way that cannot be done by direct experimentation. Interactions may be crucial in decision-making processes as different types of pig at different degrees of maturity may react differently to the same environmental stressors. There may also be differences between the response of the 'average' individual pig and the mean response of the population as a result of between animal variation (Fisher *et al.*, 1973; Ferguson *et al.*, 1997). Quantifying any differences in performance between pig types and individuals of a population may allow the removal of those constraints that prevent pigs achieving their potential under farm conditions. This in turn could have important financial implications for commercial pig enterprises.

Current pig growth models account only in part for factors affecting pig performance in commercial enterprises, which is often 20 to 30 % less than that observed under good experimental conditions (Campbell and Taverner 1985; Black *et al.,* 1999). Among the factors operating in practice that may act to limit the ability of pigs to attain their genetic potential for growth usually omitted are social stressors such as group size, space allowance and mixing, and infectious stressors. Only stressors in the physical environment such as temperature, wind speed, humidity and floor type, have been comprehensively modelled (e.g., Bruce and Clark, 1979; Black *et al.*, 1986). Only a few models have attempted to predict the performance of a population of pigs (e.g., Ferguson *et al.*, 1997; Knap, 2000a; Pomar *et al.*, 2003).

The model developed in this thesis is able to explore, and at least in principle, predict the performance of both individuals and populations of growing pigs when raised under given dietary, physical and social environmental conditions. A simplified diagrammatic representation of the model is shown in Figure GD.1.

In this Chapter the main outcomes of this thesis are outlined. Four key topics not covered in previous Chapters are then discussed. Firstly, the problem of evaluating models is discussed. A sensitivity analysis of the input parameters used in the model is also shown. Secondly, some limitations of the model developed in this thesis are

highlighted and suggestions made on how it may be improved. Thirdly, the problems associated with the estimation of parameter values are discussed. Particular reference is given to the parameter introduced in Chapter four to describe the ability of pigs to cope when exposed to social stressors, EX. Finally, the practical implications of EX in relation to production, welfare and genetic selection are considered.

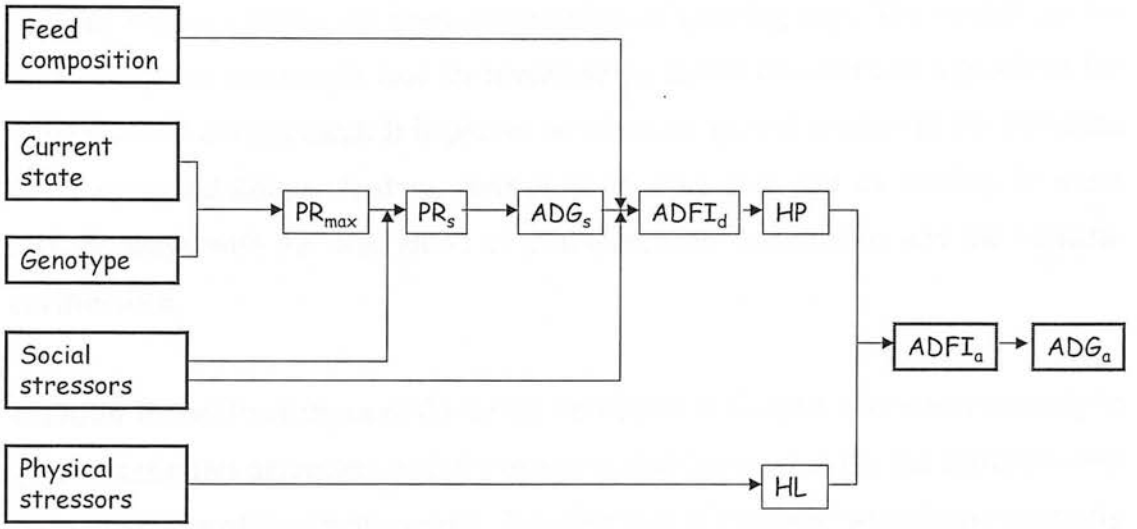


***Figure GD.1.*** *A simplified representation of the model developed in this thesis. Where PR, ADG, ADFI, HP and HL represent, protein retention, average daily gain, average daily feed intake, heat production and heat loss respectively. The subscripts max, s, d and a represent maximum, stressed, desired and actual respectively. The five boxes to the left of the diagram represent the model inputs and $ADFI_a$ and $ADG_a$ are the main outputs. $ADG_a$ is comprised of the daily gains of the individual chemical component and gut fill. For a complete description of the model see Chapters two, four and five.*

## Main outcomes of the thesis

*Chapter one:* The Gompertz function was chosen as a suitable descriptor of potential growth in the pig following a comprehensive review of the growth functions published in the literature. It has only two parameters and an initial condition, appears to hold over all degrees of maturity and has the added benefit of being able to predict the growth of the other individual chemical components of the body (lipid, water and ash) from protein by the use of allometry. Potential growth

rate is related to the genetic characteristics and current state of the individual pig only and is used as a starting point for model simulation by providing an upper limit to growth rate.

*Chapter two:* A deterministic pig growth model was developed to predict the effects of genotype, current state of the pig and the thermal and nutritional environment on the feed intake, growth and body composition of growing pigs. The model can be used as a quick and simple tool for investigation and is able serve as a platform for further model development. It improves on other pig growth models in the literature by allowing *ad libitum* feeding, compensatory lipid gain and by dealing in more realistic ways with the description of genotype, feed composition and the climatic environment.

*Chapter three:* Predictions of the model developed in Chapter two were generally in good quantitative agreement with the experimental data reported in the literature over the wide range of treatments tested. The direction of response was always correctly predicted. This gives some support to the value of the model as an effective tool for solving the problem of estimating pig performance when the thermal and nutritional environments are manipulated.

*Chapter four:* The effects of four major social stressors: group size, space allowance, feeder space allowance and mixing, on pig performance were incorporated into the growth model developed in Chapter two. Variation between genotypes in their ability to cope with social stressors was introduced and accounted for by incorporating an additional genetic parameter (EX) into the model. This adjusts both the intensity of the stressor at which the pig becomes stressed and the extent to which each stressor reduces performance and increases activity levels at a given stressor intensity. The model is an initial attempt at quantifying and predicting the generally ignored effects of social stressors on pig performance.

*Chapter five*: Between animal variation in initial state ($BW_0$), potential growth and EX was introduced into the model developed in Chapter four. Previous stochastic pig

simulation models have considered variation only in growth potential. It was assumed in the model that there is a negative correlation between $BW_0$ and EX, i.e., bigger pigs are better able to cope when socially stressed. Whether the mean population response is the same as the 'average' individual response is influenced by the way a given social stressor constrains performance. Variation in the response of a population was determined to a greater extent by variation in EX and $BW_0$ than by variation in growth potential. Consequently, decreasing the variation in $BW_0$ and improving the ability of pigs to cope may be a better way of improving pig performance than only selecting for increased potential *per se*.

*Chapter six:* A good estimate of the variation of average daily gain and feed intake of growing pigs was obtained from the data of two large-scale experiments [N = 651 and 916]. The inclusion of variation in $BW_0$ and EX into the model allowed better estimates of the phenotypic and genotypic variation observed under experimental conditions to be predicted and should be viewed as an improvement in model simulation. Variation in the growth parameters accounted for the majority of the generated variation, followed by variation in $BW_0$ and variation in EX. The model underestimated the phenotypic variation observed in the experiments. Reasons include measurement errors that cause the true phenotypic variation to be overestimated, missing information of the exact conditions applied in the treatment groups which preventing the model from being fully calibrated, and the lack of an accurate estimate of the variation present in EX within a population. In this data set only the error of measurements could be quantified.

## Model evaluation

Model evaluation is an on-going process and its primary purpose is to check the appropriateness and value of a model for predicting outcomes within the system for which it was intended (Black, 1995b). Ideally, models should predict accurately what occurs in reality. However, precise correspondence to the empirical world is not the sole reason for pursuing models. Unlike the classic concept of Popper (1972), the evaluation process of models is not as clear-cut as a simple search for 'falsification'. While it is not considered that the complexity of pig growth models makes it

impossible to prove them 'false' in any absolute sense, it does make the task of evaluation more difficult. As noted by IPCC (2001), 'it is always possible to find errors in simulations of particular variables or processes in a model'. Furthermore, any theory can always be saved by changing the values of one or more of the parameters or by adding some *ad hoc* hypothesis (Emmans, 1994b). What is important to establish is whether these errors make a given model 'unusable' in answering specific questions (IPCC, 2001). It is better to devote effort to improvement of the theory than to finding yet more ingenious reasons for the failure of facts to fit the theory (Emmans, 1994b).

Formulating a model requires specific commitments to particular theories explaining the structure and function of the phenomena being represented. This process alone, independent to the performance of the model can help clarify and refine theories about the phenomena. Once functioning, although models may not perform well enough for predictive purposes, they may still yield heuristic insights into the structure of the phenomena. Pig growth models, including the one developed here for example, while not claiming to simulate reality in every detail are able to provide valid insight into previously unrecognised issues and problems involved in pig production. For example, the introduction of the parameter EX leads to a number of questions. These include the issue of parameterisation for a given population and whether or not EX is correlated to the size of the pig, its place in the social hierarchy and/or its genotype. The general point when evaluating models and judging their scientific merit should therefore not be the sole strict criteria of accuracy but rather to offer a set of considerations that help guide researchers toward better modelling and scientific practices. 'It is by being critical of what we have now that we are pushed into going forward' (Emmans, 1994b).

### *Sensitivity analysis*

One method of model evaluation often carried out is a sensitivity analysis exercise (e.g., Lizardo *et al.*, 2002). This acts as an internal test of the model and enables the user to observe which of the input parameters the model is most sensitive to. Results of a sensitivity analysis carried out on the main input parameters of the model are

shown in Tables GD.1. and GD.2. Each parameter was increased or decreased by 10 and 20 percent relative to its default value. The responses of the sensitivity analysis were determined for the average individual pig at 60 kg over a simulation period of one day. Only the potential growth descriptors, dietary and physical environment descriptors were included in the analysis. The analysis did not include the social stressors input parameters, as the sensitivity of the model to changes in these parameters is a direct outcome of the equations formulated in Chapter four.

**Table GD. 1.** Model *sensitivity to the three parameters used to describe the potential growth of the pig (B, $P_m$ and $L_m/P_m$)*

| | Proportional change of the model parameter (%)[a] | | | | |
|---|---|---|---|---|---|
| | -20 | -10 | 0 | +10 | +20 |
| **Growth rate parameter (B; default = 0.016)** | | | | | |
| Average daily gain | -19.57 | -9.78 | 0.92 kg/d | 10.87 | 20.56 |
| Average daily feed intake | -13.79 | -6.90 | 2.03 kg/d | 7.39 | 13.79 |
| Protein deposition | -20.36 | -10.18 | 0.167 kg/d | 10.18 | 19.16 |
| Lipid deposition | -20.00 | -10.00 | 0.170 kg/d | 10.59 | 22.35 |
| Heat production | -10.60 | -5.21 | 17.46 MJ/d | 5.44 | 10.60 |
| **Mature protein mass ($P_m$; default = 32 kg)** | | | | | |
| Average daily gain | -14.13 | -6.52 | 0.92 kg/d | 5.43 | 10.87 |
| Average daily feed intake | -4.43 | -1.97 | 2.03 kg/d | 1.48 | 1.97 |
| Protein deposition | -15.57 | -7.19 | 0.167 kg/d | 5.39 | 10.18 |
| Lipid deposition | -4.12 | -2.35 | 0.170 kg/d | 0.59 | 1.00 |
| Heat production | -2.69 | -1.03 | 17.46 MJ/d | 0.69 | 1.09 |
| **Mature lipid to protein ratio ($L_m/P_m$; default = 1.2kg)** | | | | | |
| Average daily gain | -3.26 | -1.09 | 0.92 kg/d | 1.09 | 3.26 |
| Average daily feed intake | -5.42 | -2.46 | 2.03 kg/d | 2.96 | 5.42 |
| Protein deposition | 0.00 | 0.00 | 0.167 kg/d | -0.60 | -0.60 |
| Lipid deposition | -16.47 | -8.24 | 0.170 kg/d | 7.65 | 15.29 |
| Heat production | -2.41 | -1.20 | 17.46 MJ/d | 1.15 | 2.29 |

[a]Model predictions and their dimensions using default values are given in the centre column (0). The other columns indicate the variation in the model response (%) due to changes in the model parameters (%) relative to its default value. Simulations were performed on a 60-kg pig for a period of one day. Only the major output parameters sensitive to changes in the above parameters are shown.

**Table GD. 2.** Model *sensitivity to the input parameters used to describe the physical and dietary environments*

| | Proportional change of the model parameter (%)[a] | | | | |
|---|---|---|---|---|---|
| | -20 | -10 | 0 | +10 | +20 |
| **Temperature ($T_a$; default = 20°C)** | | | | | |
| Maximum heat loss | -15.76 | -7.86 | 24.17 MJ/d | 7.90 | 15.76 |
| Minimum heat loss | -23.38 | -11.69 | 12.83 MJ/d | 11.54 | 23.23 |
| **Relative Humidity (RH; default = 40 %)** | | | | | |
| Maximum heat loss | 0.87 | 0.41 | 24.17 MJ/d | -0.41 | -0.83 |
| **Wind speed (v; default = 0.15 m/s)** | | | | | |
| Maximum heat loss | -3.14 | -1.53 | 24.17 MJ/d | 1.49 | 2.90 |
| Minimum heat loss | -3.35 | -1.64 | 12.83 MJ/d | 1.48 | 3.04 |
| **Floor type[b] (default = concrete slats)** | | | | | |
| Maximum heat loss | -11.34 | -8.48 | 24.17 MJ/d | -4.51 | 8.44 |
| Minimum heat loss | -5.53 | -3.90 | 12.83 MJ/d | -1.95 | 2.96 |
| **Digestible energy content (DEC; default = 14.23 MJ/kg)** | | | | | |
| Average daily feed intake | 29.56 | 12.81 | 2.03 kg/d | -9.85 | -18.23 |
| Heat production | 2.81 | 1.20 | 17.46 MJ/d | -0.97 | -1.60 |
| **Crude protein content (CPC; default = 180 g/kg)** | | | | | |
| Average daily feed intake | -2.46 | -0.99 | 2.03 kg/d | 1.48 | 2.46 |
| Heat production | 0.57 | -0.92 | 17.46 MJ/d | 0.97 | 1.89 |
| **Crude protein digestibility ($CP_d$; default = 0.83 kg/kg)** | | | | | |
| Average daily feed intake | 2.96 | 0.99 | 2.03 kg/d | -1.48 | -2.96 |
| Heat production | 0.86 | 0.06 | 17.46 MJ/d | -0.86 | -1.83 |
| **Biological value (v; default = 0.89)** | | | | | |
| Average daily gain | 1.08 | 0.00 | 0.92 kg/d | 0.00 | - |
| Average daily feed intake | 13.79 | 6.52 | 2.03 kg/d | 0.00 | - |
| Heat production | 7.22 | 3.34 | 17.46 MJ/d | 0.00 | - |
| **Dry matter content (DMC ;default = 0.88 kg/kg)** | | | | | |
| Maximum feed intake | 25.94 | 11.52 | 3.47 kg/d | -9.22 | - |
| **Water holding capacity (WHC; default = 3 kg/kg)** | | | | | |
| Maximum feed intake | 25.07 | 11.24 | 3.47 kg/d | -8.93 | -16.71 |

[a]Model predictions and their dimensions using default values are given in the centre column (0). The other columns indicate the variation in the model response (%) due to changes in the model parameters (%) relative to its default value. Simulations were performed on a 60-kg pig for a period of one day. Only the major output parameters sensitive to changes in the above parameters are shown.

[b]Floor type (-20 = straw, -10 = wood slats, 10 = metal mesh, 20 = wet concrete).

From Table G.D.1 it can be seen that the output parameters are sensitive to all three parameters that describe the potential growth of the pig, especially the growth rate parameter, (B, $d^{-1}$). A one percent change in B resulted in an approximate one percent change in all the output parameters listed. The model predictions were least sensitive to the mature lipid to protein ratio ($L_m/P_m$, kg/kg), although lipid deposition changed significantly with a change in $L_m/P_m$. Of the physical environment descriptors the model was most sensitive to ambient temperature, although floor type also had a substantial effect on the maximum and minimum heat loss (G.D.2). Digestible energy content (DEC, MJ/kg), crude protein content (CPC, kg/kg) and biological value all effected average daily feed intake, with the model being the most sensitive to DEC. Only biological value influenced average daily gain, due to an increase in lipid deposition when v was decreased by 20 %. The dry matter content and water holding capacity of the diet both had a large effect of the maximum daily intake of the pig. However, with the default parameter values used actual daily feed intake was not constrained. From this relatively simple exercise it can be clearly seen that the model is particularly sensitive to the three pig descriptors, ambient temperature and DEC. This further highlights the importance of accurately estimating parameter values when running model simulations.

## Model limitations

Previous Chapters have discussed the main strengths of the model developed in this thesis. Here particular attention is given to the limitations of the model. Suggestions of how the model may be improved and extended to incorporate some of the omitted factors are identified and discussed.

### *Compensatory growth*

There is widespread experimental evidence that following a period of nutritional limitation that pigs are able to correct both excess (Owen *et al.*, 1971; Kyriazakis and Emmans, 1991; Kyriazakis *et al.*, 1991b) and deficit (Stamataris *et al.*, 1991) lipid in their body by showing compensatory 'thinning' and 'fattening' respectively. The model described here is one of only a few to allow for a correction to an imbalance of body lipid content. There is also evidence that depleted protein stores, along with

the closely associated water, can also be replenished (Kyriazakis and Emmans, 1991; Stamataris *et al.*, 1991) providing that the conditions of re-alimentation allow this to be achieved. It should be noted that compensatory protein gain has mainly been shown to occur in the internal organs, especially the food processing organs (FPO) whose size is directly proportional to feed intake, and not the carcass (Stamataris *et al.*, 1991; Bikker *et al.*, 1994). Some compensatory protein gain was attributed to the repletion of previously depleted labile protein stores by Kyriazakis *et al.* (1991b).

Compensatory protein gain has not been included in the model for the reasons discussed in Chapter two. Three possible mechanisms that would enable it to be incorporated are briefly discussed below. Firstly, a compensatory gain factor could be introduced into the model. This would act to multiply protein deposition in times of compensatory growth and is equivalent to the method used in the model of Black *et al.* (1986). Secondly, the model driver could be changed from protein to ash, the only chemical component of the body not shown to display compensatory growth (Kyriazakis *et al.*, 1991b; Stamataris *et al.*, 1991; Kyriazakis and Emmans, 1992d). Compensatory protein gain could then occur in the same way as compensatory lipid gain occurs in the current model, with the rate of rehabilitation being determined by constraints within the model. Such constraints include feed bulk capacity and maximum heat loss. Any interactions, such as those between the nutritional and thermal environments shown by Kyriazakis and Emmans (1991) where rates of compensatory protein gain were affected by temperature, would then be able to be predicted by the model. Lastly, body protein could be separated into FPO protein and carcass protein and a feed intake to FPO ratio incorporated. This would allow compensatory gain in FPO protein to occur in times of re-feeding whilst not affecting protein gain in the carcass. It is thought that the mechanism of modelling pig growth around ash rather protein content would be the most satisfactory method. However, this is likely to prove difficult until more information on the nutrient and energetic requirements for ash gain and the supply of the required nutrients from the diet becomes available.

### *Stress and fatness*

There is evidence in the literature that stress may affect the fatness of pigs. However, the evidence is equivocal. Morrison *et al.* (2003) and Edmonds *et al.* (1998) reported a decrease in fatness when pigs were housed in crowded as opposed to non-crowded conditions. Conversely, Chapple (1993) reported an increase in backfat depth as group size increased from one to five and Ferguson *et al.* (2001) reported an increase in lipid content with increased stocking density. Finally, Wolter *et al.* (2002; 2003) and Brumm and Miller (1996) reported no significant effect of stocking rate on carcass lean percentage or backfat depth. The effects of heat stress on fatness are again somewhat conflicting. Some authors conclude there is a decrease in fatness in hot environments (Straub *et al.*, 1976; Verstegen *et al.*, 1978; Neinaber *et al.*, 1987b; Ferguson and Gous, 1997), while others conclude an increase (Sugahara *et al.*, 1970; Holmes, 1971; Brown-Brandl *et al.*, 2000).

Most of the effects of stress, especially heat stress, are confounded with those of reduced feed intake, making it difficult to judge if there are specific stress effects on carcass fatness. In addition to slowing growth, a reduction in feed intake would be expected to lead to a decrease in fatness because of a decrease in the energy available for lipid retention after the energy requirements of maintenance and protein retention have been fulfilled. However, whilst the majority of the results can be attributed to either a decrease in feed intake or a dietary imbalance, a few cannot. For example, Morrison *et al.* (2003) implicated that the social stress resulting from reduced pen area was the cause of a decrease in backfat depth. Brown-Brandl *et al.*, (2000) reported that pigs reared in a hot environment showed an increase in carcass fatness as a result of heat stress *per se*, when compared to pair fed pigs reared in thermoneutral conditions. Finally, Le Bellego *et al.* (2002) concluded that 'heat stress has a direct negative effect on protein deposition and affects the partitioning of energy gain between protein and fat deposition'. These latter two studies appeared to account for the confounding effect of a decrease in feed intake and consequently suggest a direct stress effect on carcass fatness.

Further research on the effects of both social and heat stress on the carcass composition of growing pigs is clearly required. If there is a direct stress effect on

carcass fatness, then this could be incorporated into the model. Varying the value of the parameter that describes the lipid to protein ratio, ($L_m/P_m$), is one potential method. This would allow the fatness of the pig to change as a direct response to stress, in the same way that varying the growth rate parameter (B) alters potential protein deposition as a response to social stress. Alternatively, the rule used to determine the partitioning of energy between protein and lipid deposition may need to be altered.

*Infectious environment*

It was assumed in the model that all animals were in good health and free from exposure to infectious stressors throughout. Any response to infectious stressors, such as an increase in resource requirements to acquire and express an immune response, a change in the efficiency of energy utilisation or a voluntary reduction in feed intake (anorexia), all of which would result in a decrease in performance, were ignored. In reality of course, pigs are exposed to many different kinds and intensities of infectious stressors. These include pathogens and other harmful environmental components that may trigger tissue injury or further infection, such as other individuals in the same pen, i.e., bites and scratches.

The incorporation of infectious stressors into simulation models is an important next step in the attempt to accurately predict commercial pig performance. To include the effects of infectious stressors into a model in a systematic way it is necessary first to do a number of things. The metabolic load imposed by infectious stressors, i.e., increased nutrient requirements, and the extent to which performance is decreased need quantifying. How animals allocate resources when exposed to infectious stressors, e.g., cope with a pathogen challenge, needs investigating and the biological mechanism responsible for the decrease in performance needs elucidating. Two possible mechanisms may lead to the decrease in pig performance observed when pigs are exposed to disease. These are either a decrease in pigs' ability to attain their potential, as was assumed for social stressors in the model developed here, or a direct decrease in appetite as suggested by Kyriazakis (2003). There is also likely to be between animal variation in immune response and resilience, i.e., differences in the

ability of individual pigs to cope and perform during exposure to pathogens. This should be accounted for in any modelling attempt along with any interactions between stress and disease susceptibility.

NRC (1998) suggested that maximum protein deposition could be calculated and calibrated on an individual on-farm basis to account for variations in the health of the animals, concluding that 'it is not necessary or possible to enter other descriptions of these variables'. A more satisfactory mechanistic approach was taken by Black *et al.* (1999) who described how the effects of pleuropneumonia have been incorporated into the AUSPIG simulation model (Black *et al.*, 1986). Maintenance energy requirements were increased by up to 1.3 times normal, the rate of protein deposition decreased by 0.9 times normal and feed intake decreased down to zero depending on the severity and duration of the disease. This represents an initial step in the full representation of the physiological effects of disease in pigs and is an example of how infectious stressors may be successfully incorporated into simulation models.

Modelling the effects of the infectious environment with an understanding of the physiological mechanisms responsible for the observed effects on the animal in a manner similar to that done for the other environmental stressors, would allow interactions between genotype and the nutritional, infectious, climatic and social environments to be made.

### Estimation of model parameter values with particular reference to EX

In order for models to make valuable predictions, accurate values for the input parameters and variables are needed. However, as noted by Kyriazakis (1999) 'a major bottleneck in the development and application of all models in pig science is the process of their parameterisation'. Accurate values for the majority of the descriptors of the social, physical and nutritional environments are relatively easy to attain by direct observation and measurements. These include factors such as ambient temperature, dietary energy content and group size. Obtaining an accurate estimate of pig genotype on the other hand, which includes a description of growth potential and ability to cope when exposed to stressors, represents a major challenge.

This is in part due to the different parameters required to describe pig genotype used in different models and the difficulty associated with measuring these parameter values. Estimating the between animal variation in each of the parameter values used to describe pig genotype and any co-variation that exists between them presents an additional difficulty when simulating the response of a population. An added advantage of the Gompertz growth function is that methods to characterise the three parameters used to describe potential growth, $P_m$, $L_m/P_m$ and B, have been described by Ferguson and Gous (1993a) and Knap *et al.* (2002). The same authors, also suggest methods using simulation models to estimate the between animal variation of these parameters (Ferguson *et al.,* 1997; Knap 2000).

Currently there are no means of assigning estimates to the parameter introduced into the model developed here to describe the ability of pigs to cope when exposed to social stressors, EX. However, assuming that there is a measurable phenotypic difference between types of pigs and individuals within a population, it is thought that genetic characterisation is possible. The work of de Greef *et al.* (2003) and Kanis *et al.* (2003) supports this. They described and evaluated a conceptual framework for breeding for improved welfare in pigs and showed that it is possible to select for abilities to cope with stressors such as environmental temperature.

To satisfactorily test whether EX was useful and to quantify it by experimentation is likely to require an elaborate experiment with a large number of pigs of different breeds, strains and sexes exposed to a large number of treatments. This is unlikely to be carried out. Nevertheless, it is thought that more modest, small scale, experiments may allow first tentative estimates of both the genotype mean and between animal variation in EX to be made. Animal scientists have long been designing experiments exposing pigs of different breeds and sexes to a number of differing social stressors. These have included studies manipulating group size (e.g., Gonyou *et al.*, 1992; Spoolder *et al.*, 1999; Wolter *et al.*, 2001), space allowance (e.g., Edwards *et al.*, 1998; Hyun *et al.*, 1998), feeder space allowance (e.g., Walker, 1991; Nielsen *et al.*, 1995) and mixing (e.g., Tan *et al.*, 1991; Stookey and Gonyou, 1994). However, it has been scientists interested mainly in the behaviour of pigs that have usually

conducted these experiments. As a consequence performance measures have often been neglected or not suitably reported. For instance, no experiments in the literature where individual performance of mixed pigs has been presented could be found. The few 'mixing' experiments which reported any performance information (e.g., Hessing *et al.*, 1994; D'Eath 2002) did so only for the group. Simply including measures of performance in conjunction with the usual behavioural measures would allow progress to be made. For example, recording individual pig feed intake and gain on a daily basis for the duration of a 'normal' mixing experiment would give an indication of the effect the stresses of mixing have on individual performance. Linking the expected decreases in intake and gain due to mixing with the body weight and position of the individual within the dominance hierarchy would also allow an initial test of the assumption used in the model; that bigger pigs within the population cope best when socially stressed.

Comparing the variation in performance observed in experimental data with the variation predicted by the model will also allow an initial estimate of the variation in EX to be made. This inverted modelling technique was the method used by Ferguson *et al.* (1997) when predicting the variation in B*, $L_m/P_m$ and $P_m$. However in order for this to be successfully done a measure of the heritability of EX is also required. It is also important to know if any correlations exist between EX and any of the other genetic parameters, particularly leanness described by $L_m/P_m$. If these exist then this will affect the nature and description of the variation of the correlated parameters (Ferguson *et al.*, 1997) and would need to be accounted for in the model. This of course relies on the simplistic assumption that individuals react in the same way to all types of social stressors. However if this is incorrect, then the introduction of further parameters, in addition to EX, will be required for a sufficient descriptor of ability to cope when exposed to social stressors.

## Practical implications of EX in relation to production, welfare and genetic selection

It was predicted that variation in the growth response of a population was determined to a greater extent by variation in EX and $BW_0$ than by variation in growth potential,

when pigs were exposed to social stressors (see Chapter five). Consequently, it is suggested that the pig's potential for growth might be less important than the pig's response to stressors when pigs are reared in commercial environments. This is because improving the ability of pigs to cope would allow a greater proportion of their potential to be attained and may be a better way of improving pig performance and enterprise profitability than increasing potential *per se*. Schinckel *et al.* (2003) also noted that 'the pig's genetic potential for protein accretion and feed intake are less important than the pig's response to encountered stressors' and for these reasons suggested that 'farm x genetic population specific growth and feed intake parameters are required'.

If as suggested EX and lean growth rate are adversely correlated (Grandin, 1994; Torrey *et al.,* 2001; Schinckel *et al.,* 2003), then there may be negative implications regarding the welfare of pigs selected for lean growth. This is because selection for improved lean growth rate would indirectly lead to selection for poorer ability to cope in the population. Since EX depends in part upon the structure of the group, then group selection may be necessary in order to improve the ability of animals to cope when exposed to social stressors. Griffing (1966) found that individual selection could result in a negative response of the population mean. The experiments of Muir and Schinckel (2002) with quail and Muir (1996) and Muir and Craig (1998) with poultry, also demonstrated that selection for desirable associate effects within a group may be a means to select animals which are better adapted to their rearing environment. Any genetic correlation between EX and the growth parameters that can be evaluated could be included in the model by incorporating the co-variation between the identified parameters and EX.

Quantifying the variation in EX may improve the rate of breeding for a better ability to cope, as the amount of variation determines the degree of selection pressure able to be applied. If a parameter such as EX were included into a selection index then individual pigs with both the greatest growth potential and best ability to cope could be selected for. This would result in benefits for both welfare and production. If increased growth rate and ability to cope are antagonistic, then trying to increase pig

performance achieved under excellent conditions, i.e., improving potential alone, may not prove to be the best selection strategy. It is likely that improvements in the growth potential of the animals and in the environment, particularly better bio-security and vaccination, are required in addition to improving pigs' ability to cope.

## Contribution of this thesis to the overall issue of predicting the food intake and performance of growing pigs

In this thesis a relatively simple simulation model has been developed. It is able to explore, and at least in principle, predict the feed intake and growth performance of growing pigs when raised under given dietary, physical and social environmental conditions. In addition, it allows predictions on how between animal variation in growth potential, initial state and ability to cope when exposed to social stressors affects the performance of a population. The model provides a framework capable of being extended to incorporate other factors such as compensatory growth and infectious stressors. Some methods describing how this may be achieved have been suggested. Much work is still needed to enable pig growth models to satisfactorily predict the performance of pigs reared in commercial enterprises, but it is thought that progress has been made.

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# Publications

## Conferences

**Wellock, I.J., Kyriazakis, I. and Emmans, G.C.,** 2002. Modelling the effects of the thermal environment and dietary composition on pig performance. *Journal of Animal Science*. 80 (Supplement 1):159. (Abstract).

**Wellock, I.J., Kyriazakis, I. and Emmans, G.C.,** 2003. Modelling the effects of the thermal environment and dietary composition on pig performance. *Proceedings of the British Society of Animal Science*:72 (Abstract).

**Wellock, I.J., Kyriazakis, I. and Emmans, G.C.,** 2003. Modelling the effects of the thermal and nutritional environment on pig growth, feed intake and body composition. Pages 511-512 in *Perspectives in Pig Science.* (ed. J. Wiseman, M.A. Varley and B. Kemp). Nottingham University Press, U.K. (Abstract).

**Wellock, I.J., Emmans, G.C. and Kyriazakis, I.,** 2003. Predicting the consequences of genetic and social stress on intake and growth in growing pigs. *Book of Abstracts of the 54$^{th}$ Annual Meeting of the European Association for Animal Production:*356 (Abstract).

**Kyriazakis, I., Wellock, I.J., Emmans, G.C. and Knap, P.W.,** 2003. Consequences of genetic selection for growth and body composition on the food intake of pigs. *Book of Abstracts of the 54$^{th}$ Annual Meeting of the European Association for Animal Production:*355 (Abstract).

## Refereed papers

**Wellock, I.J., Emmans, G.C. and Kyriazakis, I.,** 2003. Modelling the effects of the thermal environment and dietary composition on pig performance: model logic and concepts. *Animal Science* **77**:255-266.

**Wellock, I.J., Emmans, G.C. and Kyriazakis, I.,** 2003. Modelling the effects of the thermal environment and dietary composition on pig performance: model testing and evaluation. *Animal Science* **77**:267-276.

**Wellock, I.J., Emmans, G.C. and Kyriazakis, I.,** 2003. Predicting the consequences of social stressors on pig food intake and performance. *Journal of Animal Science* (in press)

**Wellock, I.J., Emmans, G.C. and Kyriazakis, I.,** 2003. Describing and predicting potential growth in the pig. *Animal Science* (submitted)

"*Winning the marathon in Munich made my running, in the eyes of others, legitimate. Suddenly it was okay to be a runner, to train for 2 and 3 hours a day. There was a purpose behind it, something to be gained. My running has been looked upon as a diversion, as a particular habit for a grown man. After all, it was not earning me a decent living. It was not even making me look manly, skinny guy that I really was.*" (Frank Shorter, 1984 in *Olympic Gold. A Runner's Life and Times*).